

RESPONSE OF HEADWATER AMPHIBIANS TO LONG-TERM LOGGING
IMPACTS AND ASSESSING POTENTIAL FOR RESTORATION IN REDWOOD
NATIONAL AND STATE PARKS

By

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ABSTRACT

RESPONSE OF HEADWATER AMPHIBIANS TO LONG-TERM LOGGING IMPACTS AND ASSESSING POTENTIAL FOR RESTORATION IN REDWOOD NATIONAL AND STATE PARKS

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The timescale of community response to disturbance varies drastically, and slow-recovering ecosystems such as coastal redwood forests may take hundreds of years to return to old-growth conditions post-logging. Few studies have quantified long-term (>50 years) impacts of disturbance on ecosystems, specifically aquatic ecosystems. This study provides evidence of the persistence of historical logging impacts 50 years post-logging through the comparison of headwater amphibian populations (occupancy and abundance) and stream characteristics using a control-treatment study with a logged watershed, Streelaw Creek, as the treatment and a pristine old-growth watershed, Godwood Creek, as the control. The immediately adjacent old-growth watershed acts as a reference site because it is strikingly similar to the logged watershed including geology, orientation, topography, and forest species composition, differing only in logging history. I surveyed for the three obligate headwater amphibians in this system, which are often used as indicators for watershed quality: the coastal tailed frog (*Ascaphus truei*), coastal giant salamander (*Dicamptodon tenebrosus*), and southern torrent salamander (*Rhyacotriton variegatus*). Occupancy and abundance of headwater amphibians differed between the

logged and unlogged watersheds, with greater estimates of occupancy for all three headwater amphibians and a greater relative abundance of *D. tenebrosus* in the unlogged watershed. These results provide restoration efforts with a clear target, which is often lacking in restoration designs. These data provide baseline information for a Redwood National and State Parks project aimed at ultimately restoring the logged watershed where natural recovery has been prevented due to a combination of highly-erodible geology, low-gradient streams, and excess woody-debris from logging slash disrupting fluvial processes.

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INTRODUCTION

Disturbances to landscapes take many forms (i.e., destruction of habitat and climate change) and can be characterized as natural or anthropogenic, and by their level of intensity and severity (Resh et al. 1988, Mouillot et al. 2013). The timescale of community response to disturbance can also vary drastically. Slow-recovering ecosystems such as coastal redwood forests may take a century or more to return to old-growth conditions after logging (Russell et al. 2014). Historically, timber production was one of the most influential and widespread anthropogenic disturbances in forested landscapes, and since the mid-19th century, has been one of the major uses of forested watersheds on the north coast of California (Moyle et al. 2017). The impacts of logging practices on California watersheds have been studied since at least the 1970s, with a focus on the highly erosive watersheds on the north coast of California (Mount 1995). Chamberlin et al. (1991) found that timber harvesting may impact the form and function of watersheds in many ways including: 1) altered hydrology, 2) increased sediment delivery, 3) modified source and inputs of wood and nutrients into streams, 4) altered riparian microclimate and water temperature, 5) barriers to fish and amphibian passage, and 6) direct harm to aquatic life through the use of heavy equipment. Despite improved regulations, the legacy effects of unregulated historical timber harvest practices persist in stream ecosystems (Moyle et al. 2017).

Efforts to restore degraded watersheds in northern California began in the 1970s with the realization that populations of salmon and steelhead stocks were in peril (Lufkin

1996). The need to protect and restore the remaining stream habitat was emphasized by the recognition that healthy watersheds play an integral role in the persistence of numerous species (including humans) (Mount 1995, May et al. 1999). Since the 1980s many watershed restoration groups have been established (Mattole Restoration Council in 1983, Salmon River Restoration Council in 1992, The Watershed Research and Training Center in 1993 and Mid-Klamath Watershed Council in 2001). River restoration has continued to be a major focus of land managers and Non-governmental organizations in northern California, with the Pacific Coast having the largest number of projects and largest investment in watershed restoration in North America (Kondolf et al. 2007). However, restoration efforts and management have focused on the health of larger streams that support salmonids, and rarely on smaller headwater streams, despite their demonstrated importance as contributors to downstream biota (i.e., fish) and water quality (Moore and Richardson 2003, Meyer et al. 2007, Wipfli et al. 2007, Welsh 2011).

In a typical river drainage, headwater streams (intermittent, first- and second-order streams; all references to stream order follow the criteria of Strahler 1957) compose over two-thirds of the stream length and directly connect the upland and riparian landscape to the rest of the stream ecosystem through the transportation of matter, energy, and organisms (Freeman et al. 2007). They provide unique habitat for a wide range of animals, many of which occur nowhere else in the river system, and differ from larger streams in physical, chemical and biotic attributes; therefore, they should not be managed in the same way as large streams (Richardson and Danehy 2006, Meyer et al. 2007). Differences include smaller channel size, closed canopy, strong microclimate

gradients, higher input rates of organic matter, low primary production, low (or no) fish predation, low flows, and a disturbance regime dominated by mass failures (i.e., debris flows) (Richardson and Danehy 2006). However, their small size makes headwater streams highly sensitive to disturbance and to small-scale differences in local conditions (Meyer et al. 2007). Headwater streams warrant attention when planning stream restoration projects or assessing watershed health because they provide critical contributions to entire stream networks and are sensitive to disturbance.

The scientific interest in the development and application of ecological indicators for assessing environmental health has increased in the past 40 years (Niemi and McDonald 2004). Salmonids are widely used as indicators of watershed health, but they may be misleading indicators under some circumstances, because unpredictable variability in salmonid populations can be introduced by factors outside the freshwater system (i.e., because of migratory movements to estuaries and the ocean) (Welsh and Ollivier 1998). Frost et al. 1992 suggest that ecological indicators should be sensitive enough to anthropogenic stress that they respond in ways that are detectable, while remaining stable in unperturbed ecosystems.

Compared to fish, stream-associated amphibians are potentially more reliable indicators of watershed health because they are highly philopatric, they occur in relatively stable numbers in undisturbed environments, are relatively easy to sample, and have specialized physiological adaptations making them sensitive to disturbance (Welsh and Ollivier 1998). These attributes could allow stream-associated amphibians to indicate disturbances in watersheds at a finer or more localized scale, and with less variance,

when trying to separate natural variability in populations from the effects of anthropogenic disturbances. In addition, stream-associated amphibians could be useful indicators of watershed health because they occur throughout small watersheds, including the uppermost headwater reaches, beyond the upper range limits of salmonids. Unlike salmonids, occurrence of stream-associated amphibians in upper headwater reaches is not limited by physical attributes such as intermittent hydrology, size and depth of pools, and blockades from cascades and waterfalls (Davic and Welsh 2004).

While amphibians may lack the same economic and social values as fish, they are ecologically very important and are typically the dominant vertebrates (measured as biomass and abundance) in many small headwater streams in the Pacific Northwest (Bury and Corn 1988, Welsh and Hodgson 2008). In addition, they have evolved in the same streams with anadromous salmonids for eons, suggesting that they share similar habitat requirements in stream environments (Welsh and Hodgson 2008). For example, increased deposits of fine sediments caused by timber harvest can eliminate amphibian oviposition and refugia sites by filling interstices (Bury and Corn 1988, Corn and Bury 1989). Similarly, establishment of salmonid redds and hatching success of salmonid eggs can be negatively affected by sedimentation of gravel beds (Beschta 1978, Hicks et al. 1991). Thus, the presence of headwater amphibians may indicate the ability of a tributary network to support salmonids and other biota living down-stream (Welsh and Hodgson 2008). Although salmonids are important components of stream networks and are often the primary focus of stream restoration projects, focusing on benefits to fish alone may not properly measure the success of restoration (Jackson 2003), especially in small

headwater streams. When defining habitat quality in small headwater streams, comparisons with fish-bearing streams should not be used, and instead habitat quality should be determined by the habitat needs and preferences of amphibians and macroinvertebrates, which comprise the top trophic levels in headwater streams (Jackson and Sturm 2002). Using amphibians as indicators of restoration potential or success could provide a more reliable and comprehensive representation of watershed conditions.

Redwood National and State Parks (RNSP) in Humboldt County, California, initiated a watershed restoration program in Redwood Creek in 1978 (RNSP 1999, Madej et al. 2006). The parks have employed various restoration efforts including revegetation of previously logged areas (Madej et al. 2006) and a massive program that removed ~ 425 km of roads through a range of techniques (abandonment to full recontouring) within the park boundaries (Seney and Madej 2015). However, the use of headwater amphibians to design restoration projects or monitor restoration success has been minimal. While research has been conducted on headwater amphibians in the Redwood Creek watershed (Welsh and Ollivier (1998), Ashton et al. (2006), Cannata et al. (2006), Madej et al. (2006) and Wilzbach (2016)), no baseline data are available on headwater amphibian populations at the site of RNSP's next planned watershed restoration project, which will take place in the Streelow Creek watershed.

Currently, RNSP are in the initial stages of a restoration project designed to ultimately restore the Streelow Creek watershed, which was degraded by historical logging practices, to pre-logging conditions. The Streelow Creek watershed was heavily logged between the late 1940s and early 1960s (Wilzbach 2016). Logging in this

watershed employed timber harvest practices highly detrimental to aquatic ecosystems, including clearcutting along the stream, tractor yarding in streams, and construction of roads, skid trails, and landings in the riparian zones (Best 1995). Logging in the Streelow Creek watershed ceased in 1968 when the Redwood National Park was established (RNSP 1999). However, impacts to aquatic ecosystems from unregulated logging in the Streelow Creek watershed were amplified due to floods (particularly in 1955 and 1964) that caused widespread erosion and sedimentation (Madej 1995).

Since logging ceased in the Streelow Creek watershed, no replanting or thinning of the second-growth forest occurred (RNSP 2007). Water quality is assumed to have improved because soils should have stabilized with reestablishment of forest vegetation, particularly along stream-sides (RNSP 2007). However, despite 50 years for natural recovery, the Streelow Creek watershed remains largely in a degraded state compared to adjacent tributaries (Wilzbach 2016), presumably as a result of the watershed's highly erodible geology, the predominately low stream gradients, and continued input from unrestored source areas (Cannata 2006, Wilzbach 2016). In addition, excessive logging slash in the form of coarse woody debris (CWD) and remaining roads and skid trails appear to have disrupted natural fluvial processes, specifically the transportation of sediment (pers. obs.).

Frequently, restoration efforts are hampered by lack of information on baseline conditions, and as a result, inadequate determination of the desired future conditions towards which restoration efforts should be directed (National Research Council 1992). In addition, it is often difficult to perform ecological experiments at large spatial scales,

so land managers often rely on observation, inference or models to guide their understanding of a system (Resetarits and Bernardo 1998). However, in this case, an immediately adjacent unlogged old-growth watershed, Godwood Creek, provided an unusual opportunity for a retrospective paired-watershed study design to accurately assess impacts and appropriate restoration goals for the degraded Streelow Creek watershed.

Godwood Creek watershed is an unlogged old-growth watershed that lies in Prairie Creek Redwood State Park immediately adjacent to Streelow Creek (Figure 1). Besides its logging history, Godwood Creek is very similar to Streelow, including orientation, drainage size, stream gradient, channel form, topography, geology, and forest species composition, all of which are factors that can influence the occurrence of headwater amphibians in watersheds on the north coast of California (Diller and Wallace 1999, Adams and Bury 2002). The geomorphological similarity between Streelow Creek and Godwood Creek watersheds presents an opportunity for inquiry into what stream habitat conditions and stream-associated amphibian populations were in the Streelow Creek watershed prior to logging, and to assess changes caused by historic logging activities. A comparison of the stream-associated amphibian populations and their associated habitat characteristics in the Streelow Creek and Godwood Creek watersheds can be utilized as an indicator of watershed health or ecological disturbance. This study will also provide a method for quantification of the effects of historic logging in the Streelow Creek watershed.

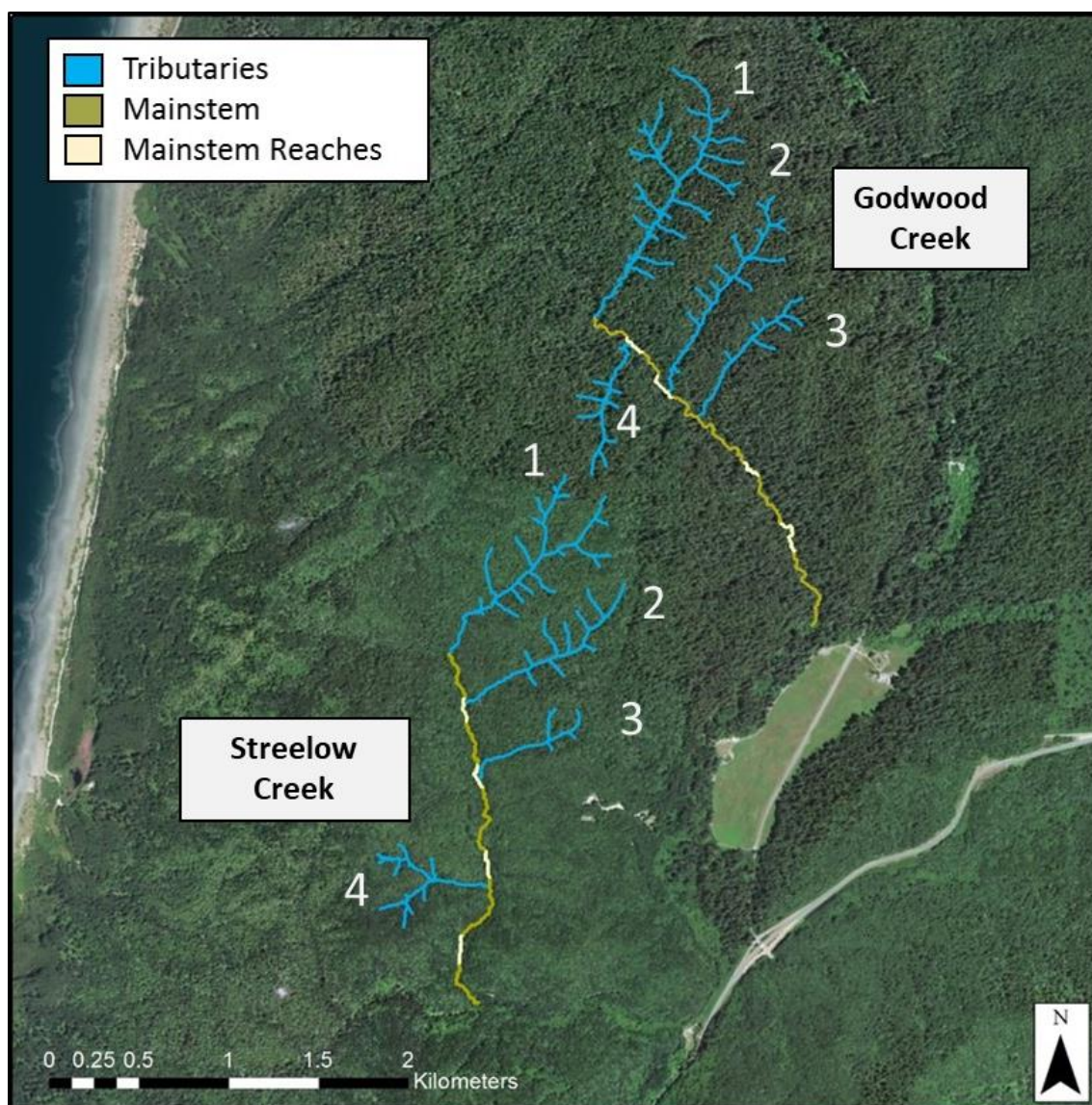


Figure 1. Map showing the two sample tributaries, Streelow Creek (logged) and Godwood Creek (unlogged). Paired tributaries are marked 1-4.

Objectives

My overarching goals for this research were to provide RNSP with a more comprehensive understanding of the Streelow Creek watershed (logged) and to provide crucial pre-project base-line data on headwater amphibians and their associated habitat characteristics prior to carrying out restoration of Streelow Creek. The data generated will also provide insight into the potential for amphibian recovery in Streelow Creek following habitat restoration. To achieve these goals, I addressed two key research questions.

First, I assessed how past logging practices may have altered amphibian populations and their associated habitat characteristics through comparison between the Streelow Creek and Godwood Creek watersheds. If effects from logging persist in the Streelow Creek watershed, I expected to find differences in the abundance, distribution, occupancy and body condition of headwater amphibians between the watersheds. Specifically, I expected to find greater occupancy, abundance, and body condition indices (BOCI) and wider distribution of headwater amphibians in the unlogged Godwood Creek. I also expected to find differences in stream habitat characteristics between the watersheds, including higher sediment cover and lower coarse cover in Streelow Creek. If watershed characteristics (i.e., drainage size, orientation, stream gradient, channel width) are similar between the watersheds, this could suggest that substantial differences in amphibian populations and their associated stream habitat characteristics are likely a

result of differences in logging histories and not inherent differences between the watersheds.

Second, because a substantial amount of the amphibian populations may have been lost at Streelow Creek, I determined locations of remaining populations of amphibians and the associated condition of their habitat. These data can be used to identify areas best suited for future restoration and as a baseline to assess the success of future restoration efforts. For example, sites near source amphibian populations may present high potential for restoration, while immediate areas with remnant amphibian populations may be poor locations for restoration actions given the risk of the loss of individuals or even populations.

STUDY SITE

This retrospective treatment-control study was conducted in RNSP, in Humboldt County, northwestern California. RNSP consists of Redwood National Park and three state parks (Prairie Creek Redwoods, Del Norte Coast Redwoods and Jedediah Smith Redwoods), which together protect the largest contiguous stand of ancient (primary) coast redwood forest (RNSP 1999). The study sites were in the Prairie Creek sub-basin of Redwood Creek (Figure 2). The Prairie Creek sub-basin is a fourth-order tributary that runs for 20 km almost entirely within the boundaries of RNSP (Cannata et al. 2006). Prairie Creek is the largest of the Redwood Creek tributaries, entering 5.6 km upstream from the mouth (Wilzbach 2016).

A complete description of the climate, vegetation, and geology of Prairie Creek sub-basin is provided by Sparkman et al. (2014), which I summarize here. The climate is mild due to its low elevation and proximity to the Pacific Ocean. The mean annual precipitation is 177 cm and most rain falls between November and March. Peak flows occur during winter, as summer discharge is not affected by snowmelt. The remaining portions of old growth forests are dominated by the coastal redwood (*Sequoia sempervierens*). Other tree species found in the watershed included Sitka spruce (*Picea sitchensis*), tanoak (*Lithocarpus densiflorus*), madrone (*Arbutus menziesii*), big-leaf maple (*Acer macrophyllum*), California bay laurel (*Umbellularia californica*), and red alder (*Alnus rubra*). The understory consisted of salal (*Gaultheria shallon*), sword fern (*Polystichum munitum*), redwood sorrel (*Oxalis oreganan*), rhododendron

(*Rhododendron macrophyllum*), azalea (*Rhododendron occidentale*) and huckleberry (*Vaccinium* spp.). Most of the Prairie Creek sub-basin, including where Streelow and Godwood Creek watersheds, is underlain by the Prairie Creek Formation (Cashman et al. 1995). This formation has distinctively sharp ridges, steep canyons, a trellis drainage pattern and is characterized by weakly-consolidated shallow marine and alluvial sediments (and coarse alluvial sequences) that appear to be remnant of the lowermost reaches of the ancestral Klamath River (Cashman et al. 1995). The Prairie Creek watershed is considered to have some of the highest uplift and seismic activity rates in North America because the entire watershed is situated on a tectonically active and geologically complex area (Sparkman et al. 2014). Three major faults cut through the Prairie Creek formation including the Grogan, Lost Man, and Sulfur Creek faults (Cashman et al. 1995). The highly erodible geology, weakly consolidated soils, high precipitation, and steep topography of the Prairie Creek sub-basin (Cashman et al. 1995) exacerbate the erosional process, increasing the potential for high levels of fine sediment (Cannata et al. 2006).

This study was limited to two of the western tributaries of the Prairie Creek sub-basin, Streelow Creek (10T 421871, 4554349) and Godwood Creek (10T 413753, 4579767) (Figure 2). In Streelow Creek, surveys were conducted in the North Fork because the drainage size and orientation were most similar to Godwood Creek. In addition, persistent impacts from past logging practices were most evident in the North Fork of Streelow (pers. obs.). For convenience, North Fork Streelow will be referred to as simply ‘Streelow’ throughout the rest of this thesis. Prior to logging, Streelow was a

redwood dominated forest, but after logging the forest around Streelow was a dense stand of second growth coast redwood, Douglas fir (*Pseudotsuga menziesii*) and was dominated by Sitka spruce (RNSP 2007). Streelow drains around 3 km² with old-growth trees making up less than 14% of the forest (Wilzbach 2016). Godwood Creek is a coastal redwood dominated watershed that drains 4.6 km² and <1% of this area has been previously logged (Wilzbach 2016). For simplicity, I will refer to Godwood Creek as ‘Godwood’ hereafter. Both watersheds have gentle gradients at their heads with broad, flat-floored valleys that provide habitat for anadromous salmon (Cannata et al. 2006). The most distinctive difference between the two watersheds is their logging history.

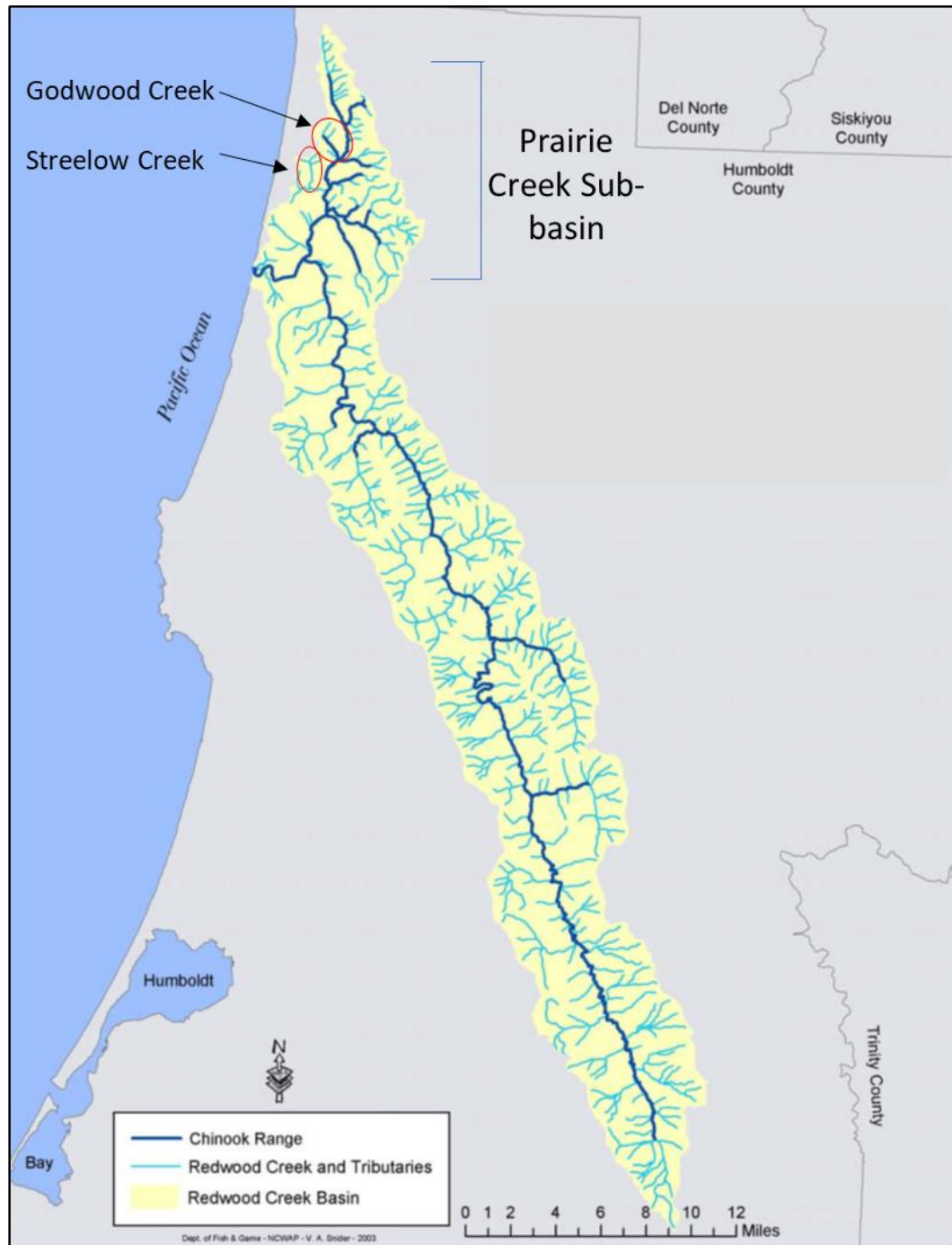


Figure 2. Map adapted from Cannata et al. (2006). Location of watersheds within Redwood Creek circled in red. Streelow Creek (logged) and Godwood Creek (unlogged) are tributaries of Prairie Creek, the largest tributary of Redwood Creek.

Study Species

Redwood-forested watersheds in northern California have three obligate headwater amphibian species: the Coastal Giant Salamander (*Dicamptodon tenebrosus*), the Southern Torrent Salamander (*Rhyacotriton variegatus*), and the Coastal Tailed Frog (*Ascaphus truei*) (Nussbaum et al. 1983). All three of these species require year-round cold water for completion of their egg and larval cycles (Nussbaum et al. 1983) and are sensitive to impacts from logging such as increased sediment loads (Welsh and Ollivier 1998).

Dicamptodon tenebrosus

Dicamptodon tenebrosus are one of the four closely related species in the family Dicamptodontidae (Stebbins 2003). Their range extends from British Columbia to northwestern California (Bury and Corn 1988) and the species occurs in both aquatic and terrestrial morphs (Nussbaum et al. 1983). *Dicamptodon tenebrosus* have a complex life history, where some aquatic larvae do not metamorphose into terrestrial adults, and instead reach adult size and become sexually mature, while retaining their larval characteristics (i.e., paedomorphosis) (Nussbaum et al. 1983). Those individuals that do metamorphose are not tied to stream channels and can travel long distances from streams (Johnston and Frid 2002).

The larval period lasts anywhere from 2 to 6 years (Leonard et al. 1993), during which they feed on a wide range of organisms, including fish, invertebrates, tadpoles and other *D. tenebrosus* (Nussbaum et al. 1983, and Parker 1994). They occur in a variety of

streams, ranging from headwater (first-order) streams down through larger fish-bearing (fifth-order) streams, but are more commonly found in first-order streams (Welsh and Hodgson 2008). In small streams, they are the dominant vertebrate predator and can comprise over 95% of the predator biomass (Murphy and Hall 1981). They occupy a wider range of habitats than *A. truei* or *R. variegatus* and have a much broader temperature tolerance (Bury and Corn 1988, Welsh and Hodgson 2008). Increased abundance of *D. tenebrosus* can be associated with large woody debris, coarse substrate, and stream gradient, but the effect that these variables have on *D. tenebrosus* varies (Bury and Corn 1988, Corn and Bury 1989, Welsh and Hodgson 2008) and they are often considered a habitat generalist (Welsh and Ollivier 1998).

Ascaphus truei

Ascaphus truei are one of two members of the family Ascaphidae, which is the most basal clade of extant anuran families (Ford and Cannatella 1993), and they are listed as a species of special concern by California Department of Fish and Wildlife (CDFW). They are endemic to and occur throughout the Pacific Northwest from sea level to high elevations near timberline, and their occurrence in streams often overlaps with the upper limits of some salmonid species (Nussbaum et al. 1983). *Ascaphus truei* often do not occur in the uppermost headwater reaches as do *R. variegatus*, suggesting that *A. truei* are more likely to be influenced by the indirect cumulative effects of logging practices (Diller and Wallace 1999). Reports on the effects of logging on *A. truei* populations vary (Corn and Bury 1989, Diller and Wallace 1999, Jackson 2003, Wahbe and Bunnell 2003), but, larval *A. truei* are associated with higher gradient riffles and coarse substrate,

and do not occur in stream sections that have been impacted with high levels of fine sediment (Corn and Bury 1989, Diller and Wallace 1999). Adults can move through adjacent forested areas between streams (Wahbe et al. 2004), whereas larvae have relatively limited vagility and live most of their lives in or immediately adjacent to a relatively short reach of stream (Matsuda and Richardson 2005, Burkholder and Diller 2007).

Tadpoles have an enlarged oral disc that is an adhesive sucker-like structure, which enables them to adhere to rocks in fast-flowing streams and to scrape diatoms from rocks (Metter 1964). In northern California, tadpoles have a larval period between one and two years (Bury and Adams 1999, Wallace and Diller 1999), requiring permanent rocky streams that are cool and well oxygenated year-round (Vlaming and Bury 1970, Corn and Bury 1989). Regardless of the length of the larval period, larvae in north coastal California typically metamorphose during late summer low flows (Diller and Wallace 1999). Burkholder and Diller (2007) suggested a biannual reproductive cycle.

Rhyacotriton variegatus

Rhyacotriton variegatus are endemic to the Pacific Northwest and occur in conifer-dominated forests in coastal ranges from northern Oregon to Mendocino County in northern California (Good and Wake 1992, Stebbins 2003). *Rhyacotriton variegatus* are the southernmost member of the family Rhyacotritonidae (Good and Wake 1992) and are listed as a species of special concern by CDFW. *Rhyacotriton variegatus* are patchily distributed in forest seeps, headwater springs, first-order forested streams and along the margins of larger streams (Welsh and Lind 1996, Nussbaum et al. 1983, Stebbins 2003,

Tait and Diller 2006). They tend to be found in the interstices of substrate and under moss and organic debris (Good and Wake 1992, Leonard et al. 1993). *Rhyacotriton variegatus* have a relatively long development time, with the time from egg to metamorphosis taking 2-2.5 years (Tait and Diller 2006). While the larval form breathes through a combination of cutaneous respiration and gills and is entirely aquatic, the adult form is capable of upland movement and can utilize moist riparian and forested areas (Nussbaum et al. 1983). However, *R. variegatus* adults often occur in the same stream habitat as larvae (Nussbaum et al. 1983, Tait and Diller 2006).

Rhyacotriton variegatus are associated with high stream gradients (Diller and Wallace 1996), low sedimentation (Welsh and Ollivier 1998), coarse substrate, forested canopy cover >80% (Welsh and Lind 1996) and cold-water temperatures (Diller and Wallace 1996, Welsh and Lind 1996, Corn and Bury 1989). Because *R. variegatus* occur in a relatively narrow range of physical and microclimatic conditions, they may be highly vulnerable to direct impacts from timber harvest, such as excessive canopy removal or sediment deposits from heavy equipment operation (Bury and Corn 1988; Corn and Bury 1989; Diller and Wallace 1996). Populations may be slow to recolonize after a disturbance such as logging because of their patchy distribution and low rates of population growth (due to prolonged larval periods and low fecundity rates) (Tait and Diller 2006).

METHODS

This study was designed as a retrospective treatment-control study using a mid-seral stage watershed degraded by past logging practices (Streelow), as the treatment and a late seral pristine watershed (Godwood), as the control. I implemented a stratified-random survey approach within the stream channels to assess the impacts of logging on amphibian populations and their habitat. The proportion of the stream reaches surveyed and the survey protocol varied intra- and inter- watershed, due to the differences in fluvial processes and proportion of exposed channel among the tributaries and mainstem. Published protocols are based on streams with obvious pool riffle delineations and easily accessible channels (Diller and Wallace 1999, Welsh and Ollivier 1998), which was not the case in these watersheds, and required modification of existing protocols.

I defined two channel types, tributaries and mainstem channels, based primarily on differences in fluvial processes and the resulting channel morphologies. Mainstem channels were third-order channels of the watersheds surveyed; these were lower gradient (0-1%) and had relatively wider channels, with a more obvious pool-riffle delineation than tributary channels. Tributary channels were first- and second-order channels that ran into the mainstem of each watershed. Tributary channels tended to have steeper gradients (>5%) towards the headwaters, more confined channels, and tended to be influenced by colluvial inputs more than by fluvial processes, resulting in ambiguous pool-riffle distinctions. The headwater portions of tributary channels in both watersheds tended to

run subsurface, or were buried under mass amounts of large woody debris, making the channels inaccessible for surveys.

I surveyed the mainstem and four tributaries in the control and treatment watersheds (Figure 1). I selected the four tributaries in each watershed by pairing tributaries that had similar drainage size, aspect, geology, gradient and shape. I selected these geomorphological variables because they may affect the presence and distribution of stream-associated amphibians (Diller and Wallace 1996, Adams and Bury 2002). I used a stratified-random approach to delineate 4, 200-m reaches throughout the beginning, middle, and end of each mainstem channel. In the tributaries, I surveyed throughout the entirety of each of the eight reaches (total tributary lengths ranged from ~ 0.3 to ~1.5 km). Tributary surveys began at a random point within 30 m of the confluence (with the mainstem) and continued into the upper headwaters until the tributary channel could no longer be identified.

I conducted field work with a 2-4 person crew from 22 May – 31 August in 2016 and from 6 July – 9 August in 2017. Due to higher summer flow rates in 2017, I delayed surveys until early July when the flows were comparable with summer 2016 flows. I utilized flow recordings from a gauge at the mouth of Redwood Creek to estimate when flows were comparable (USGS 2017). I collected data for two seasons to characterize inter-annual variation.

Surveys in mainstem and tributary reaches consisted of four main components: 1) mapping, 2) habitat sampling surveys, 3) amphibian surveys, and 4) systematic stream samples (SSS). Mapping surveys were conducted continuously throughout the watershed,

habitat sampling and amphibian surveys were conducted within the same area-constrained units, and SSS were conducted every 50 m along the channel. Temperature and flow measurements were also measured throughout the watersheds.

Mapping

The goal of mapping was to create a continuous profile of habitat characteristics that could be used to test for differences between Streelow and Godwood. To create this profile, I measured two variables, channel type and woody debris, while walking upstream throughout the entirety of each mainstem and tributary reach. I recorded the locations of these variables as the distance (in m) from the beginning of the reach (always the most downstream portion).

Channel type was divided into four categories: open, subsurface, buried, or pocket. I recorded the length and location (start and end) of each channel type, unless the section was less than 1 m. If water was present in the channel and a surveyor could access the channel to perform a habitat or amphibian survey, I described the channel as ‘open’ (Figure 3). In mainstem reaches, I further characterized open sections as either slow-water (SW) or fast-water (FW), and recorded the start and end of each section (Figure 3). Slow-water sections were composed of pools, runs, or slack water (Figure 3-a), and FW sections were composed of riffles, cascades or any area with noticeable surface disturbance (Figure 3-b). To aid in stratified sample unit delineation for amphibian and habitat surveys, SW and FW sections were divided into roughly 5-m units and every third 5-m SW and FW unit was flagged and sampled for habitat variables (see section Habitat

Sampling Survey). In tributary reaches, open sections were not further characterized as SW and FW due to ambiguous pool-riffle distinctions.



Figure 3. Examples from study site showing a) a slow-water (SW) section in Streelow Creek (logged) and b) a fast-water (FW) section in Godwood Creek (unlogged). Both pictures also show the reach type ‘open’ (water was present in the channel and a surveyor could access the channel to perform a habitat or amphibian survey).

If all or part of the channel disappeared from view, it was designated as either subsurface, buried or pocket, and the start and end of each section was recorded. I described the channel as ‘subsurface’ if the channel disappeared and running water could not be heard below the surface. If the channel disappeared, but flow could still be heard below the surface, I described the channel as ‘buried’ (e.g., dense amounts of wood covering the channel made it inaccessible for surveying) (Figure 4). And lastly, channels

were designated ‘pocket’ if subsurface sections were frequently interspersed with less than 1 m sections of open channel.



Figure 4. A section of a mainstem reach in Streelow Creek (logged) that was characterized as ‘buried’ channel. Water can be seen at the bottom left of the photo, but the channel is inaccessible for surveys due to the large number of downed trees.

I recorded the amount and size of all in-channel woody debris with a diameter >15 cm (measured at the thickest part of the wood piece) and a length of >1 m. I divided wood into two categories: large woody debris (LWD) or spanners (SPAN), based on the impact the wood had on the fluvial process of the channel. I described LWD as any piece of downed wood within the bankfull that had the potential to affect the fluvial process (i.e., within bankfull) of the stream channel. Wood type SPAN spanned the width of the channel and did not appear to affect the fluvial process of the stream. I further divided LWD and SPAN into size classes based on length and diameter, categorizing diameters as small = 15-30 cm, medium = 30-50 cm, and large = 50+ cm; and length as short = 1-6 m and long > 6 m. I did not record the exact location of each piece of wood because of

the excessive amount of time required, and instead recorded the total amount of specific LWD and SPAN size classes within every FW or SW unit in the mainstem reaches, or within every 50 m in the tributary reaches. I only recorded wood in open-channel sections.

Habitat Sampling Surveys

Mainstem reaches

Habitat sampling surveys were placed into roughly 5-m units within SW and FW sections (units varied between 3-6 m depending on length of each FW or SW section). For example, a 10-m FW section would be made up of 2 5-m FW units (Figure 5). At the beginning of each mainstem reach, I randomly chose to start surveying the first, second, or third FW or SW unit and then systematically surveyed every 3rd FW or SW unit. If a survey unit occurred in an area that was obstructed by objects such as downed wood that made surveying difficult or dangerous, I moved the unit to the next closest SW or FW unit.

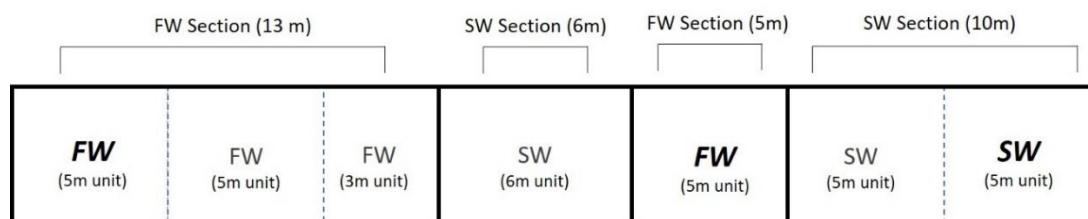


Figure 5. Diagram demonstrating the sampling layout in mainstem reaches where fast-water (FW) and slow-water (SW) sections were further delineated into approximately 5-m sections and every 3rd FW and SW unit were flagged and sampled (bolded units represent sampled units). Note the differences in unit lengths due to differences in section lengths. In this scenario the 1st FW and the 3rd SW units were randomly chosen as starting points.

At each habitat sampling unit I placed start and end flagging (marked with the unit number) to provide a visual boundary for the surveyor and to allow me to return to the exact location to conduct repeat surveys. I recorded the length of the survey unit, the location, and the unit type (SW or FW). I also measured habitat variables at 3 cross-sections set across the width of the channel. I placed the first sample cross-section in the middle of the unit and the last 2 cross-sections in the middle of the first and second half of the unit.

At each cross-section, I recorded wetted width (cm) (width of the stream channel), depth (at $\frac{1}{4}$, $\frac{1}{2}$, and $\frac{3}{4}$ of the way across each cross-section), overhanging cover (total linear length of living or dead vegetation and bank cover up to 1 m above the water line), unit gradient ($^{\circ}$) and substrate cover (clay, fines, sand, gravel, pebble, cobble, small woody debris and LWD). I recorded substrate cover at every 2 decimeters along the cross-sections using a classification of substrate particle size (modified from Cummins 1962). I avoided surveyor bias of substrate cover by using a “blind touch” technique where the surveyor places a finger on the substrate directly below a point without looking at the substrate. Substrate was measured along the shortest axis. I recorded the unit gradient within each unit by placing a TripleMag digital level-bevel gauge onto a collapsible 3-m painting pole that was held parallel to the water surface angle.

Tributary reaches

I systematically conducted habitat surveys with the goal of surveying one unit every 50 m in tributary reaches. If stretches of non-open channel extended for longer than

50 m, this resulted in a deficit of unit surveys. When open channel was reached, I conducted consecutive unit surveys until I reached an average of 1 survey/50 m of stream length. This protocol resulted in a nearly-complete survey of the exposed channel in reaches with high amounts of subsurface, buried and pocket sections. Survey units were between 2-3 m long (no less than 2 m but preferably 3 m in length) and the start of the unit was placed at exactly 50 m. Just as in the mainstem reaches, the start and end of each unit was flagged, and the same protocol was utilized for habitat surveys.

Seeps

To generally characterize seeps, I gathered substrate cover every 10 m or wherever a *R. variegatus* was found. If seeps were less than 10 m, I measured substrate cover at a random distance from the start of the seep. I measured substrate cover with a 15 X 15 cm metal grid with 5 cm mesh. I quantified the substrate cover (same as mainstem and tributaries) at each grid cross-section, resulting in 12 substrate measurements (Diller and Wallace 1996). I also characterized the overall gradient of the seep by taking gradient measurements at each obvious slope change using the same technique as in the mainstem and tributaries.

Systematic Stream Samples

I used Systematic Stream Samples (SSS) to quantify similarities in watershed morphology between Streelaw and Godwood. To document watershed morphologies, I conducted an SSS every 50 m along mainstem and tributary reaches, regardless if the stream was open, subsurface, or buried. At each SSS I measured valley-slope, valley-

width, canopy cover, stream gradient, and an additional habitat sampling survey. If an SSS survey randomly occurred at a buried or subsurface section, I did not conduct a habitat sampling survey or record the stream gradient.

I recorded the slope gradient ($^{\circ}$) of each valley slope using a clinometer. I used a 50 m measuring tape and a rangefinder to quantify valley-width, which I defined as the sum of the perpendicular distance from the middle of the stream to where there was an obvious increase in slope. I estimated canopy cover at each SSS with a convex spherical densiometer read at the four cardinal directions from the middle of the channel. To reduce recording overlap caused by the curved-reflective surface, I followed the Strickler (1959) method where 79 of the 96 dots were covered to leave a wedge shape of 17 dots, and the number of points in the wedge-shaped area that was covered by canopy was recorded at each cardinal direction. I measured stream gradient with a clinometer by measuring to another surveyor staged at least 10 m away. This method characterized the general gradient of the stream channel, differing from the unit gradients gathered in the habitat sampling surveys that only captured the gradient of the specific sample unit.

Amphibian Surveys

D. tenebrosus and *A. truei* surveys

Amphibian surveys were primarily focused on the larval stages of *D. tenebrosus* and *A. truei* because larvae are closely tied to stream channels, while metamorphosed adults are not. Adult stages of both species were encountered and their presence was recorded but not used in analyses. Survey protocols for *D. tenebrosus* and *A. truei* were

the same in mainstem and tributary reaches and took place in the same units as habitat surveys. I conducted amphibian surveys before taking habitat measurements following a light-touch sampling technique, a type of visual encounter search where a surveyor searches the streambed and under easily movable objects on the substrate surface (Hayes et al. 2006). This light-touch method reduced the disturbance to the amphibians and the stream and required less effort (per unit area) than traditional ‘rubble-rousing’ techniques where all moveable substrates (i.e., rocks, boulders, and woody debris) are removed from the stream bed and placed on the adjacent bank (Bury and Corn 1991, Quinn et al. 2007). Furthermore, this light-touch method allowed me to survey more units while still conducting repeat surveys and has been used for surveying long stretches of streams where amphibian populations are patchily distributed (Quinn et al. 2007).

Each survey was started on the downstream unit end to avoid increased turbidity, thereby preserving visibility in the survey unit. Surveys were area-constrained and were considered complete once the observer had surveyed throughout the entire unit and under all moveable substrate for animals. Surveys lasted from 2-60 min, with longer surveys at units with wide channels, high complexity, and large amounts of coarse substrate where animals could hide in the numerous interstices. To decrease the probability of double-counting individuals and to allow for further measurements, I attempted to capture every animal that was detected during the initial survey (% capture for *D. tenebrosus* = 0.50; capture for *A. truei* % = 0.76; % capture for *R. variegatus* = 0.60).

Surveys were conducted with one person standing outside of the channel recording data, and one person in the channel searching for amphibians. The recorder

documented the start and end time of each survey and the time-to-detection (minutes after start of survey) for every animal detected, whether it was caught. The in-channel surveyor used a viewing bucket and aquarium net to visually search a unit and to capture amphibians. Viewing-buckets were made from 5- or 3-gal buckets with plexiglass bottoms (larger buckets were used in mainstem reaches and smaller buckets in small tributaries). In slow-water (SW) sections, surveyors walked slowly through the channel using a viewing bucket to see the channel bottom while simultaneously turning over all moveable objects (coarse woody debris, cobbles, and small boulders) that were not embedded in the channel. When an amphibian was detected, the surveyor used the aquarium nets to scoop up any amphibians seen on the channel bed or that had become dislodged while overturning objects. In fast water (FW) sections, the surveyor employed a technique where in addition to utilizing the viewing bucket, the surveyor held an aquarium net immediately downstream of an area of the stream bed they had lightly disturbed with their hand. The surveyor used the aquarium net to catch dislodged animals being carried downstream. I did not use block nets because of the overall low gradient and flow of the watersheds.

All captured amphibians were carefully placed in a plastic bag filled with cold stream water and placed in the shade until the end of the survey. Substantially larger *D. tenebrosus* were placed in separate bags to eliminate the potential for predation on smaller larvae. I measured the snout-vent length (mm) (from the tip of the snout to the middle of the cloaca) for all captured *D. tenebrosus* and the total length (mm) (from the tip of the snout to the tip of the tail) for all captured *A. truei*. All animals were measured

to the closest millimeter with a plastic ruler inside of plastic bags. Additionally, I recorded weights of all animals caught during the 2017 field season so I could calculate body condition indexes (BOCI). BOCI are body mass measurements that have been corrected for body size (body mass/body length) and are thought to indicate the health of an individual (amount of energy reserves) (Welsh et al. 2008). Animals that inhabit a low-quality habitat may have lower BOCI through physical stresses that reduce foraging success (Welsh et al. 2008). I recorded weights with a 30-g Pesola scale to the closest tenth of a gram. Animals were weighed in plastic bags and the weight of the bag and any excess water was subtracted from the final weight. All animals were immediately placed back into the channel after measurements were taken.

I conducted repeat amphibian surveys at one third of the units in mainstem reaches, 1-3 days after the initial survey, to estimate detection probability (in some cases we conducted repeat surveys at 100% of the units due to the limited amount of exposed channel). Amphibians may go undetected due to surveyor inexperience, cryptic behavior, or complex habitat, and thus estimates of detection probability may be necessary to permit comparison of amphibian abundance or site occupancy when detection probability is less than 1 (MacKenzie et al. 2002). I assigned repeat survey units by implementing a stratified random approach where surveys were partitioned equally between SW and FW units. Again, I recorded time-to-detection for all individuals detected, but I did not capture individuals because I did not want to re-measure individuals that were measured in the initial survey. I did not conduct repeat surveys in tributary reaches due to limited access and difficulty of movement.

R. variegatus surveys

I did not specifically survey for *R. variegatus* in the mainstem or tributary reaches, although juveniles and adults were found in these channels. Alternatively, I surveyed for *R. variegatus* in any off-channel seeps or springs that were found along mainstem or tributary reaches. I surveyed for both the adult terrestrial and larval aquatic morph because the adults are often found in the same habitats as the larvae. When I found a seep, I marked a UTM location at the bottom of the seep (often the confluence with the main or tributary channel) with a Garmin GPS. To determine *R. variegatus* presence, I conducted discrete survey trials where I systematically searched each seep for a max of 10 min or stopped when the first *R. variegatus* was found. I measured the same variables recorded in the *D. tenebrosus* and *A. truei* surveys for each *R. variegatus* caught.

Previous studies on *R. variegatus* did not conduct repeat surveys due to the destructive nature of the surveys and assumed a high but unknown detection probability (Diller and Wallace 1996, Welsh and Lind 1996, Russell et al. 2005, Ashton et al. 2006). Therefore, I did not conduct standardized repeat surveys to estimate detection probabilities. However, throughout the season I observed that my survey methods caused very little disruption to seep habitat and could potentially warrant repeat surveys, so I conducted non-random repeat surveys at 4 seeps (Streelaw = 1, Godwood = 3) during the 2017 field season. At all 4 seeps, I detected *R. variegatus* during both survey occasions. Additionally, at the end of the 2016 field season, I noted that 4 seeps (Streelaw = 3, Godwood 1) where no *R. variegatus* were found were dry and likely could not support *R.*

variegatus. Although only a small number of non-random repeat surveys were conducted, the outcome suggests that detection probability was close to 1 in these seeps.

Flow

I used a float method described by Dobriyal et al. (2017) to approximate flow at least twice in all mainstems and tributary reaches. The float method has low accuracy but is time efficient, cost effective, and is suitable for small streams with low flow (Dobriyal et al. 2017). Additionally, the relative difference was the focus of comparison and therefore high accuracy readings were not essential. I recorded flow measurements at locations where the channel was the most amenable to accurate recordings (level channel bed, uniform channel width for 1-3 m, and flowing water sections with enough water to float an object down without disturbance). I marked the start and end of the test area and recorded the total length (travel distance, 1 - 3 m). I dropped a natural floating object into the channel just upstream of the starting marker and recorded the time (sec) it took the object (usually an *Oxalis* leaf) to reach the end marker. I repeated this at least 3 times and averaged the measurements to get the average travel time. I then recorded the channel width (m) at three locations and channel depth (m) at $\frac{1}{4}$, $\frac{1}{2}$ and $\frac{3}{4}$ of the way across the channel.

2017 Field Season

During the 2017 field season, I surveyed a third of the units that were surveyed in each mainstem and tributary reach during the 2016 field season. I used a stratified

random approach to delineate units to be surveyed evenly between the SW and FW units in the mainstem reaches and evenly among the beginning, middle and end of the tributary reaches. At each unit surveyed, I conducted a habitat and amphibian survey and I conducted repeat surveys at 100% of the units surveyed in the mainstem reaches. I did not conduct additional *R. variegatus* surveys. I also did not conduct additional SSS because the measurements were unlikely to change between years. I recorded flow again at roughly the same locations flows were taken during the 2016 field season. Additionally, I conducted a water temperature profiling survey.

Watershed temperature profiling

I deployed 24 iButton temperature loggers throughout both watersheds from 26 July to 2 September to determine if there were differences in stream temperatures. The iButtons recorded temperature to the nearest 0.1 C° at 1-hr intervals each day. Because iButtons are not made to be submerged in water, I waterproofed them by covering each unit with 3 layers of Plasti-Dip, and then placed it in 50-ml conical centrifuge tubes. I deployed one iButton in each mainstem reach (8 total) and placed two iButtons at the beginning and middle of each tributary reach (16 total). I used wire to attach the conical centrifuge tubes to stationary objects (i.e. roots, embedded wood or large rocks) at the bottom of deep pools (around an arms-lengths in depth in the mainstem reaches and ~1/2 m in depth in the tributary reaches) where we expected the channel would not become dewatered.

Statistical Analysis

Watershed comparison analysis

I compared physical variables gathered during habitat surveys and systematic stream samples (SSS) between Streelaw and Godwood. I used the Wilcoxon rank-sum test to test for differences between watersheds for most variables, because data were not distributed normally. Some of the calculated p-values were not exact, due to ties. I tested for normality using a Shapiro-Wilks test for normality and for homogeneity of variance (HOV) using Levene's Test. I used Cliff's delta (<0.147 = negligible, <0.33 = small, <0.474 = medium, >0.474 = large) from the 'effsize' package in R (Torchiano 2017) to calculate effect sizes for nonparametric parameters. To compare normally distributed variables, I used the student's t-test and Cohen's d (<0.2 = negligible, <0.5 = small, <0.8 = medium, >0.8 = large) from the same 'effsize' package in R to estimate effect size. Comparisons were made at multiple scales including at the watershed scale, between mainstem and tributary reaches, and between paired reaches. Other purely descriptive variables such as flow and water temperatures were not compared using a statistical test, but instead summarized in tables and graphs for comparison. I used medians with the IQR (inter-quartile range) for graphical representations of non-normal data and means with SE or 95% confidence intervals (CI) as error bars for normal data. I pooled the data across years during the analysis for all variables except for unit gradient and temperature, which I only collected during one field season.

To compare substrate cover, I grouped all the substrate types into four categories: sediment (clay, fines, sand), gravel, coarse (pebble, cobble) and wood (LWD and SWD). I averaged % overhang, channel depth, and wetted width across the 3 belts within each

survey unit for comparison. I calculated canopy cover at each SSS by multiplying the sum of the cardinal direction recordings by 1.5 and then subtracting 2% to account for error (associated error considered unimportant for comparison of relative values) (Strickler 1959). Raw values of unit gradient, stream gradient, valley-width and valley-slope were used for comparison.

For the woody debris comparison, I averaged the number of pieces of woody debris per 1 km in all size classes (woody debris type, diameter and length) and by diameter size class (1, 2, 3). For reach composition I compared the proportion of each reach type (open, subsurface, buried, and pocket) at each scale. I also calculated the composition of FW and SW units within the open channel sections and the average length of FW and SW units. I calculated flow using the formula $Q = AV$, where Q = stream discharge (Volume/Time), A = cross-sectional area, and V = flow velocity. A was calculated as the product of the average depth and average width of the float section. V was calculated as the product of the average float travel time and the length of the float area. To account for channel bed roughness I multiplied V by a roughness coefficient of 0.85 (IEI 2016). To convert to cfs (ft³/sec) I multiplied Q (m³/sec) by the conversion factor 35.3147.

Headwater amphibian analysis

At each unit surveyed I calculated the relative index of abundance for *D. tenebrosus* as the number of individuals detected at unit/unit area (m²). I calculated the number of individuals as the maximum number of individuals found at a unit (maximum during the initial and repeat surveys of both field seasons) and I calculated the area as the

product of the unit length and the average unit width. I compared the relative index of abundance between watersheds graphically (mainstem and tributary scale) and with a Wilcoxon rank-sum test. Additionally, I utilized maximum likelihood methods to create single-species, single-season occupancy models to estimate site occupancy (Ψ) and detection probability (p) of *D. tenebrosus* and *A. truei* as a function of habitat characteristics (MacKenzie et al. 2002).

Occupancy is defined as the probability that a randomly selected site or sampling unit in an area of interest is occupied by a species (MacKenzie et al. 2002). In this study, occupancy is defined as the probability that a randomly selected sampling unit in Streelaw or Godwood is occupied by *D. tenebrosus* or *A. truei*. Site occupancy of *D. tenebrosus* and *A. truei* was estimated using the unmarked package in R (Fiske and Chandler 2011, 2017). I assessed the goodness of fit for occupancy models using a parametric bootstrap method suggested by Fiske and Chandler (2017). I pooled occupancy data over both field seasons and assumed closure of sites throughout the seasons and across years. I considered 4 observation-level covariates and 10 site-level covariates as potential covariates for detection and occupancy probabilities of *D. tenebrosus* or *A. truei* (Table 1). I fit models with and without covariates to the data and ranked the models according to AIC (Burnham and Anderson 2002). Because this was a paired study design, all models fit with covariates included the variable Pair.ID.

Table 1. Description of covariates used in the single-species, single-season occupancy models for *D. tenebrosus* and *A. truei*. Variables used in *R. variegatus* logistic regression models are also included in the table.

Observation -Level Covariates	Description	Site-Level Covariates	Description
Tmax	Total time of survey (minutes)	Watershed	Streelow or Godwood Creek
Obs	Observer	Tier	Mainstem or Tributary
MOD	Minute of Day – Time survey start calculated as minutes since 0900	Pair.ID	Numerical value 1-5 given to paired tributary and mainstem reaches
Year	Year survey was conducted (2016 or 2017)	Coarse	% of unit composed of substrate type pebble or cobble.
		Gravel	% of unit composed of substrate type gravel
		Wood	% of unit composed of SWD or LWD
		Over	% overhanging vegetation
		Grad	Gradient of unit/seep

I did not calculate *R. variegatus* relative index of abundance, and instead mapped the distribution of occupied and unoccupied seeps throughout both watersheds. I did not utilize occupancy models to estimate occupancy for *R. variegatus* because I only conducted single surveys at each seep. Instead, I assumed detection probabilities were close to 1 and used a logistic regression to test the relationship between occupied seeps and measured habitat variables. I used AICc to compare the candidate models because the sample size was small ($n/k < 40$ with k = number of fitted parameters in the global model) (Symonds and Moussalli 2011). I utilized the function ‘aictab’ in the R package ‘AICcmodavg’ to calculate the AICc scores (Mazerolle 2017). I model-averaged using the function ‘modavg’ from the same ‘AICcmodavg’ R package and tested the model fit

of all top models with the Hosmer-Lemeshow goodness of fit test (function ‘`hoslem.test`’) from the R package ‘ResourceSelection’ (Lele et al. 2019).

Post hoc, I considered using a time-to-detection occupancy model (Garrard et al. 2008) that does not require repeat surveys at the same site like traditional occupancy models. Instead, this approach uses the time-to-detection (TTD) of a species to: 1) estimate detectability, 2) model TTD as a function of an encounter rate parameter and 3) model the TTD/encounter rate parameter function as a function of covariates (Bornand et al. 2014). However, because some unoccupied seeps were surveyed for less than 10 min (short seeps with high sediment cover), I could not estimate an encounter rate parameter. To estimate the encounter rate parameter of this model, surveying all seeps for a set amount of time or until the first *R. variegatus* was found would have likely helped.

Lastly, I compared the snout-vent-lengths (SVL) and Body Condition Index (BOCI) of *D. tenebrosus* between the watersheds. I graphically compared SVL with density distribution plots and compared BOCI residuals from an ordinary least squares regression ($\log(\text{weight}) \sim \log(\text{SVL})$) with a Wilcoxon rank-sum test. Sample sizes were too small in Streelaw to compare size measurements and BOCI of *A. truei* between watersheds, but density distribution graphs with data from both watersheds are reported in Appendix A.

RESULTS

During the 2016 field season, I surveyed for headwater amphibians in a total of 236 units with 138 of those units in tributary reaches (Streelow = 45 units; Godwood = 93 units), and 98 of the units in mainstem reaches (Streelow = 43; Godwood = 55) (Appendix B.1). I conducted repeat surveys at 39 (42%) of mainstem reaches. During the 2017 field season, I conducted repeat surveys at a total of 86 units with 54 of those units in tributary reaches (Streelow = 24; Godwood = 30) and 32 units in mainstem reaches (Streelow = 16; Godwood = 16) (Appendix B.2). I conducted repeat surveys at all 32 units in mainstem reaches.

Watershed Habitat Variable Comparison

Valley-slope, valley-width and stream gradient

I recorded measurements for valley-slope at 160 locations in Streelow (n = 70) and Godwood (n = 90). There was a positive association between distance up the tributary reaches and gradient of the valley-slope (Figure 6-a). The valley-slope differed between the watersheds ($W = 1516.5$, $p < 0.001$; Cliff's delta = -0.519, 95% CI [-0.65, -0.35]) with a consistently steeper valley slope in Godwood (median = 26°; Streelow median = 21.5°) (Figure 6-b). However, there was no difference in valley-slope when comparing just mainstem reaches (Figure 6-b) (Streelow median = 15°; Godwood median = 20°; $W = 75$, $p = 0.479$; Cliff's delta = -0.167, 95 % CI [-0.64, -0.40]), but the sample size was small (Streelow: n = 12; Godwood: n = 154). Valley-slopes were different at the

tributary reach scale (Streelow median = 21.1° ; Godwood median = 26.4° ; $t = -7.39$, $p < 0.001$, $df = 105.11$; Cohen's $d = -1.333$, 95% CI [-1.71, -0.95]).

I recorded valley-width measurements at 163 locations in Streelow ($n = 70$) and Godwood ($n = 93$). Contrary to valley-slope, valley-width had a negative relationship with the distance up the tributary reaches (Figure 6-c). Valley-width differed between the watersheds ($W = 2660$, $p = 0.046$), with a median valley-width of 12 m in Streelow and 16 m in Godwood, but the effect size was small (Cliff's $\delta = -0.183$, 95% CI [-0.34, -0.02]). The largest difference was between the mainstem reaches ($t = -5.64$, $p < 0.001$, $df = 23.15$, Hedges's $g = 2.13$, 95% CI [1.13, 3.13]) where the mean valley-width in Godwood ($\bar{x} = 93.82$ m) was 53 m wider than in Streelow ($\bar{x} = 40.92$ m) (Figure 6-d). There was no difference between tributary reaches ($W = 1904.5$, $p = 0.1156$; Cliff's $\delta = -0.158$, 95% CI [-0.34, 0.03]), with a median valley-width of 10 m in Streelow and 13 m in Godwood.

I recorded stream gradient at 81 locations in Streelow ($n = 24$) and Godwood ($n = 57$). The mainstem reaches in both watersheds were low-gradient streams that ranged between 0° and 2° . The gradient was higher in tributary reaches than in mainstem reaches but still similar between the watersheds with a range between 0 and 5.5° .

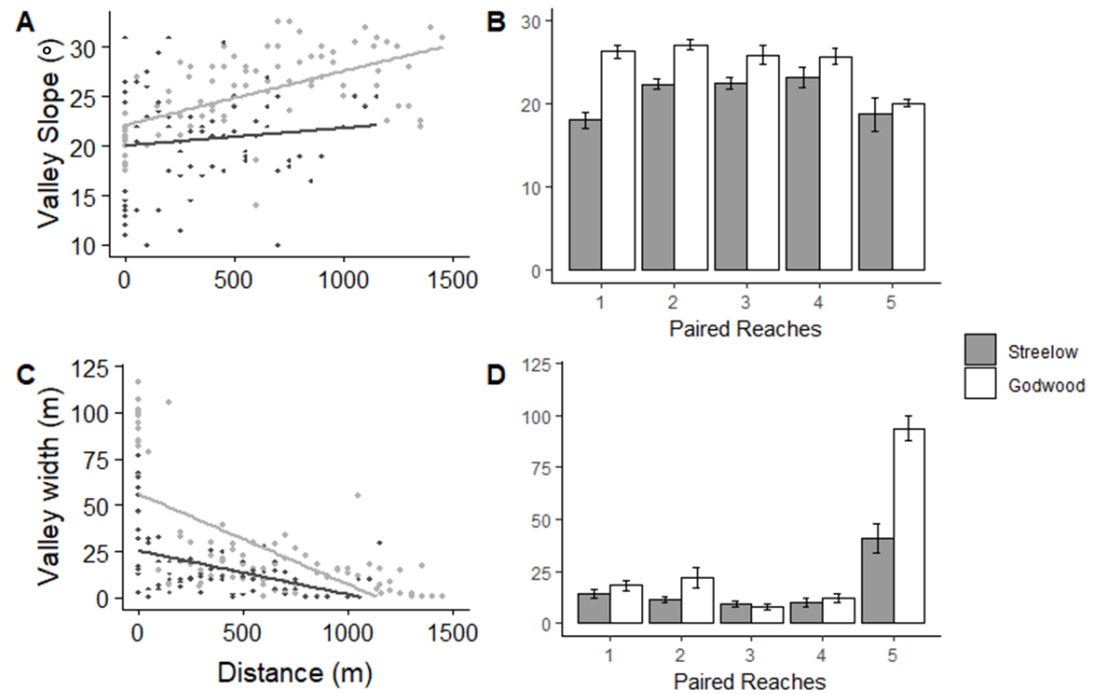


Figure 6. Comparison of valley-slope and valley-width between Streelow (logged) and Godwood Creeks (unlogged). Panels a) & c) show relationship of valley-slope/width with distance up tributary reaches (from where it meets mainstem), while b) & d) median valley-width/valley-slope at paired reach scale (mainstem unit distance = 0). Paired reaches 1-4 are tributary reaches, and paired reaches 5 are mainstem reaches. Error bars = IQR.

Depth, wetted-width and unit gradient

I recorded channel depth at 353 units throughout Streelow ($n = 139$) and Godwood ($n = 214$). At all scales there was no difference in channel depth between watersheds ($W = 15916$, $p = 0.266$, Cliff's delta = 0.070, 95% CI [-0.05, 0.19]). The median channel depth in mainstem reaches was 15.22 cm in Streelow and 16.67 cm in Godwood. In tributary reaches the median channel depth was 4.39 cm in Streelow and 4.44 cm in Godwood. The median depth of SW units was 22.67 cm in both watersheds. The median depth of FW units was 8.56 cm in Streelow and 11.95 cm in Godwood.

I recorded wetted-width at 356 locations units throughout Streelow (n = 140) and Godwood (n = 216). At the watershed scale there was no difference in wetted-width ($W = 13378$, $p < 0.066$, Cliff's delta = -0.115, 95% CI [-0.23, -0.01]) between Streelow (median = 91.17 cm) and Godwood (median = 112 cm). However, there was a difference between the watersheds at the tributary or mainstem scales. The wetted-width of tributaries in Streelow (median = 0.62 m) was smaller than the tributaries in Godwood (median = 0.84 m) ($W = 3469$, $p < 0.0001$), but the effect was small (Cliff's delta = -0.316, 95% CI [-0.45, -0.16]). The wetted-width in mainstem reaches of Streelow (median = 1.85 m) was also smaller than mainstem reaches in Godwood (median = 2.48 m) ($W = 1565$, $p < 0.0001$, Cliff's delta = -0.393, 95% CI [-0.55, -0.21]), with the median wetted-width in Godwood 0.63 m wider than in Streelow.

I recorded unit gradient at 243 locations throughout Streelow (n = 93) and Godwood (n = 150). The unit gradient of Streelow ranged from 0-4.15°, with the mainstem reaches ranging from 0-3.25° and no obvious correlation between upstream portions of the tributaries and steeper unit gradients. The unit gradient of Godwood ranged from 0-9°, with most of the steeper unit gradients occurring at the uppermost portions of the headwaters. The gradient in the mainstem units of Godwood only ranged from 0-4°. Both watersheds were low gradient with the mean unit gradients around 1-2°.

In Streelow the seep gradient ranged from 8.5° to 20° in the mainstem reaches and 6° to 30° in the tributary reaches. In Godwood, the seep gradient ranged from 5.35° to 13.05° in the mainstem reaches and 1° to 30° in the tributary reaches. There was no difference between the mainstem and tributary reaches within Streelow ($t = -0.832$, $p =$

0.471, $df = 2.78$; Cohen's $d = -0.503$, 95% CI [-1.82, 0.81]) or Godwood ($t = -0.968$, $p = 0.34$, $df = 25.24$; Cohen's $d = -0.262$, 95% CI [-1.21, 0.68]). Additionally, there was no difference between the mainstem reaches of Streelaw ($\bar{x} = 13.8^\circ$) and Godwood ($\bar{x} = 8.6^\circ$) but there was a difference between the tributary reaches with steeper seep gradients in Streelaw ($\bar{x} = 16.9^\circ$, Godwood: $\bar{x} = 10.7^\circ$; $t = 2.65$, $p = 0.012$, $df = 38.38$; Cohen's $d = 0.80$, 95% CI [0.13, 1.46]). Lastly, there was no difference in gradient between occupied and unoccupied seeps (occupied = 12.85° , unoccupied = 12.83° , $t = 0.01$, $p = 0.994$, $df = 42.17$; Cohen's $d = 0.002$, 95% CI [-0.57, 0.58]).

Canopy cover and % overhang (vegetation)

I recorded canopy cover at 177 locations throughout the Streelaw ($n = 77$) and Godwood ($n = 100$) watersheds. The canopy cover in Streelaw was high, with a median canopy cover of 97.06%. The canopy cover was lower in Godwood (median = 88.24%) at all scales except in one paired watershed (watershed scale: $W = 1974.5$, $p < 0.0001$, Cliff's delta = 0.487, 95% CI [0.33, 0.62]). The range of canopy cover values in Streelaw was small with 50% of the values between 91% and 98.5%, whereas in Godwood 50% of the values were between 80.5% and 95%.

I recorded % overhang at 354 units throughout Streelaw ($n = 139$) and Godwood ($n = 215$). The % overhang was consistently lower in Streelaw at all scales (watershed scale: $W = 9951$, $p < 0.0001$, Cliff's delta = -0.334, 95% CI [-0.45, -0.21]) with a 29.78% median overhang in Streelaw and a 44.19% median overhang in Godwood. The median % overhang in the mainstem reaches was 21.21% in Streelaw and 33.67% in Godwood ($W = 1509$, $p < 0.001$; Cliff's delta = -0.406, 95% CI [-0.56, -0.22]). In the tributary

reaches the median percent overhang was 39.13% in Streelow and 53.84% in Godwood ($W = 3806$, $p = 0.004$, Cliff's delta = -0.244, 95% CI [-0.40, -0.07]). In both watersheds the median % overhang was higher in the tributaries than in the mainstem reaches but the effect was small (Streelow: $W = 3504.5$, $p < 0.0001$, Cliff's delta = 0.455, 95% CI [0.27, 0.60]; Godwood: $W = 7697.5$, $p < 0.001$, Cliff's delta = 0.449, 95% CI [0.30, 0.57]).

Substrate cover

I surveyed percent substrate cover at 354 units throughout Streelow ($n = 139$) and Godwood ($n = 215$), including surveys conducted during SSS. At all scales, the units surveyed in Streelow had higher percent sediment cover (sand and fines) (median = 28.6) than Godwood (median = 6.9) (watershed scale; $W = 23110$, $p < 0.0001$, Cliff's delta = 0.547, 95% CI [0.434, 0.642]) (Figure 7-a). Conversely, the percent of coarse substrate cover (pebble and cobble) was lower at all scales in Streelow (watershed scale: Streelow median = 21.6%; Godwood median = 60%, $W = 4063.5$, $p < 0.0001$, Cliff's delta = -0.728, 95% CI [-0.80, -0.63]) (Figure 7-b). There was a difference in percent gravel cover at the watershed scale ($W = 17523$, $p = 0.006$), with higher percent gravel cover in Streelow (median = 32.3%) than in Godwood (median = 24.3%), but the effect size was small (Cliff's delta = 0.173, 95% CI [0.043, 0.297]) (Figure 7-c). Lastly, there was a difference in percent wood cover between watersheds ($W = 20696$, $P < 0.0001$, Cliff's delta = 0.385, 95% CI [0.27, 0.49]), with higher percent wood cover in Streelow (median = 6.9) than in Godwood (median = 0) (Figure 7-d).

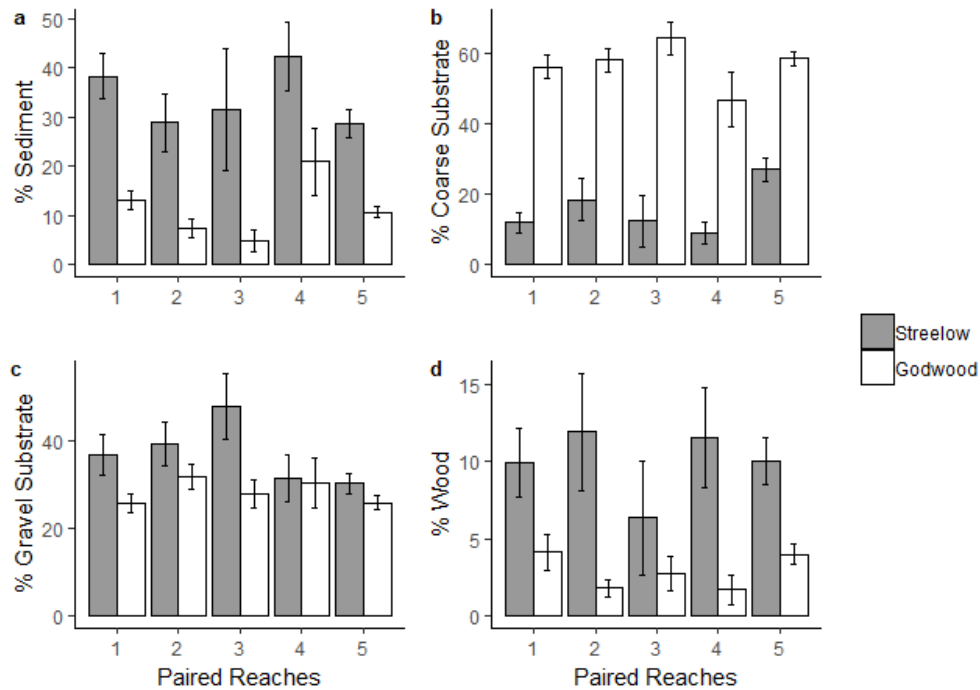


Figure 7. Comparison of percent substrate cover between Streelow (logged) and Godwood Creeks (unlogged) at the paired reach scale (Pair 1-5 = Tributaries; Pair 5 = Mainstem). Panels: a) mean % cover of sediment (clay, fines and sand), b) mean % cover of gravel, c) mean % cover of coarse (pebbles and cobbles), and d) mean % cover of wood (LWD and SWD) at surveyed units. Error bars = +/- SE.

The dominant seep substrate types in Streelow were gravel (median cover = 33.3%) followed by a mix of fines (median cover = 14.5%) and pebble (median cover = 14.4%) (Figure 16). In Godwood, gravel (median = 50%) and pebbles (median = 18.8%) were the dominant substrate types (Figure 8). The 3 seeps that were found in the mainstem reaches of Streelow were composed entirely of sediments and SWD.

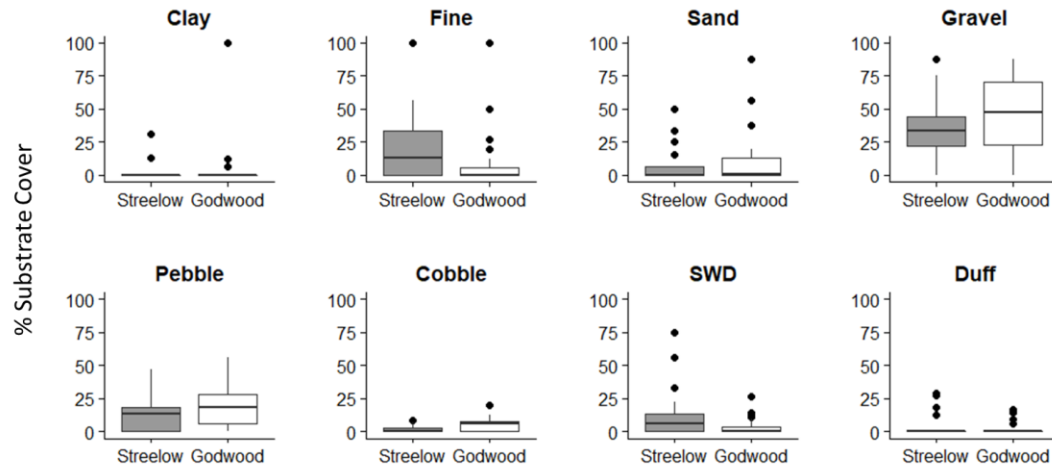


Figure 8. Comparison of the substrate cover (clay, fines, sand, gravel, pebbles, cobble, SWD and duff) of seeps between Streelow (logged) and Godwood Creek (unlogged).

Reach composition

The composition of channel types (open, subsurface, buried, and pocket) was similar between mainstem reaches of both watersheds with open channel composing 86% of mainstem reaches in Streelow and 99% in Godwood (Figure 9-a). Within the open sections of the mainstem reaches in Streelow, the composition of fast-water (FW) and slow-water (SW) was similar (FW = 48.5%, SW = 51.5%) whereas in Godwood the composition of FW was 13% higher (FW = 61.1%, SW = 48.5%). Additionally, the median length of FW sections was shorter in Streelow (median = 9) than in Godwood (median = 15 m; $W = 507$, $p = 0.01$, Cliff's delta = -0.408, 95% CI [0.10, 0.65]), but SW sections were similar in length (Streelow median = 6.2 m, IQR = 9.6; Godwood median = 10, IQR = 7.1; $W = 573.5$, $p = 0.06$, Cliff's Delta = 0.291, 95% CI [-0.01, 0.54]).

Compared to the mainstem reaches, the tributary reaches in both watersheds had higher proportions of subsurface, buried and pocket channel types (Figure 8). In Streelow, 33.8% of tributary channels were open, 46.3% were subsurface, 8.3% were buried and 11.6% were pocket (Figure 9-b). In Godwood, 66.2% of tributary channels were open, 21.8% were subsurface, 7.5% were buried, and 4.5% were pocket (Figure 9b).

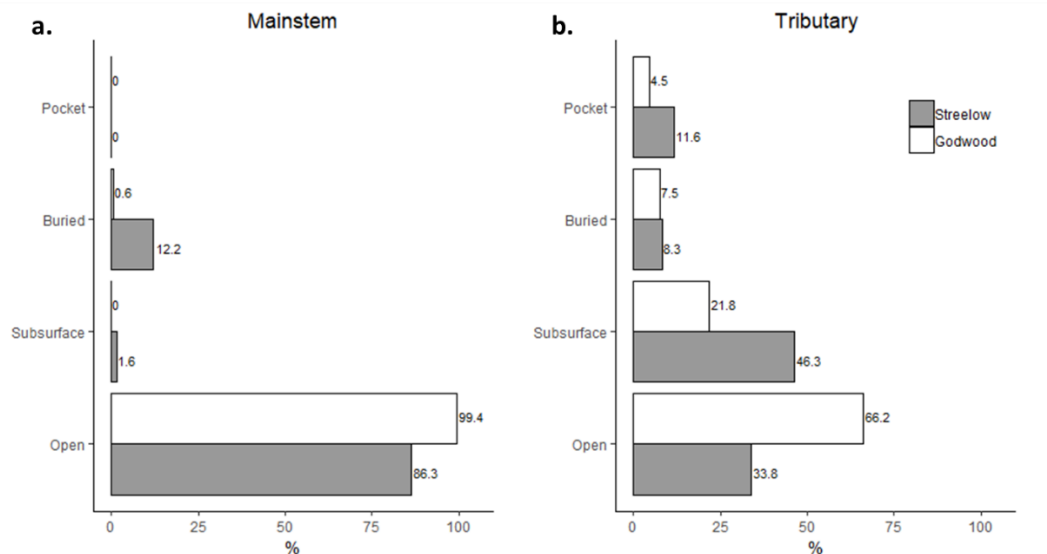


Figure 9. Comparison of percent composition of each reach type (open, subsurface, buried and pocket) in the mainstem (a) and tributaries (b) of Streelow (logged) and Godwood Creek (unlogged).

I mapped the distribution and amount of subsurface, buried and pocket reach types using ArcGIS (Appendix C). Many tributary reaches in Streelow were subsurface, buried or pocket, with the open sections concentrated near the confluence with the mainstem. Subsurface, buried and pocket sections can also be seen in the tributary reaches in Godwood, but most of these reach types were only evident in the uppermost headwater reaches of the watershed and were interspersed with open channel.

Woody debris

A broad-scale comparison of the total average number of woody debris pieces per km (all size classes and types grouped together) at the watershed scale showed there were more woody debris in Streelaw ($\bar{x} = 27.3$, 95% CI [24.5, 30.1]) than in Godwood ($\bar{x} = 16.0$, 95% CI [14.6, 17.4]; $t = 7.17$, $df = 5028.2$, $p < 0.0001$, Cohen's $d = 0.17$, 95% CI [0.13, 0.22]) (Figure 10-a). Interestingly, a comparison of the average number of woody debris per km between diameter size classes showed there was no difference in the largest diameter size class (size 3) between Streelaw ($\bar{x} = 23.6$, 95% CI [19.2, 28.0]) and Godwood ($\bar{x} = 22.2$, 95% CI [19.4, 24.9]; $t = 0.54$, $df = 1970$, $p < 0.59$, Cohen's $d = 0.022$, 95% CI [-0.05, 0.10]) (Figure 10-b). However, within the SPAN type woody debris there were less long, large diameter pieces (SPAN 3L) in Streelaw ($\bar{x} = 14.4$, 95% CI [6.7, 22.1]; than in Godwood ($\bar{x} = 42.6$, 95% CI [35.5, 49.7]; $t = -5.29$, $df = 655.2$, $p < 0.0001$, Cohen's $d = -0.39$, 95% CI [-0.54, -0.24]) (Figure 10-a).

A finer scale comparison between the mainstem reaches of the watersheds show there were more woody debris in the mainstem reaches of Streelaw ($\bar{x} = 30.3$, 95% CI [26.2, 34.4]) than in Godwood ($\bar{x} = 10.17$, 95% CI [8.0, 12.4]; $t = 8.50$, $df = 2990.4$, $p < 0.0001$; Cohen's $d = 0.27$, 95% CI [0.21, 0.34]) (Figure 10-c & -d). In both the watersheds there were more LWD (Streelaw: $\bar{x} = 16.3$, 95% CI [12.13, 20.48]; Godwood: $\bar{x} = 16.79$, 95% CI [12.72, 20.86]) than SPAN (Streelaw: $\bar{x} = 43.94$, 95% CI [37.08, 50.81]; Godwood: $\bar{x} = 3.56$, 95% CI [1.96, 5.14]) in the mainstem reaches (Streelaw: $t = -6.75$, $df = 1606.5$, $p < 0.0001$; Cohen's $d = -0.31$, 95% CI [-0.40, -0.22]; Godwood: $t = -5.94$, $df = 1370.4$, $p < 0.0001$; Cohen's $d = -0.26$, 95% CI [-0.34, -0.17]) (Figure 10-c).

At the tributary reach scale there was no difference in the average number of woody debris between Streelaw (Streelaw: $\bar{x} = 23.2$, 95% CI [19.8, 26.6]) and Godwood ($\bar{x} = 19.7$, 95% CI [17.9, 21.5]; $t = 1.82$, $df = 2196.7$, $p = 0.068$, Cohen's $d = 0.063$, 95% CI [0.00, 0.13]) (Figure 10-e & -f). However, there was a difference in the size class SPAN-3L between the watershed, with lower amounts in Streelaw ($\bar{x} = 14.4$, 95% CI [6.67, 22.14]) than in Godwood ($\bar{x} = 42.6$, 95% CI [35.54, 49.74]; $t = -5.29$, $df = 655.23$, $p < 0.0001$; Cohen's $d = -0.39$, 95% CI [-0.54, -0.24]). Contradictory to the mainstem reaches, there were more SPAN (Streelaw: $\bar{x} = 16.3$, 95% CI [12.13, 20.48]; Godwood: $\bar{x} = 22.6$, 95% CI [19.91, 25.28]) than LWD (Streelaw: $\bar{x} = 43.9$, 95% CI [37.08, 50.81]; Godwood: $\bar{x} = 16.7$, 95% CI [14.42, 19.03]) in the tributary reaches of Streelaw ($t = -2.48$, $df = 1324.7$, $p = 0.013$) and Godwood ($t = -3.26$, $df = 3274.9$, $p = 0.001$), but the effect sizes were small (Streelaw: Cohen's $d = -0.13$, 95% CI [-0.24, -0.03]; Godwood: Cohen's $d = -0.11$, 95% CI [-0.18, -0.04])

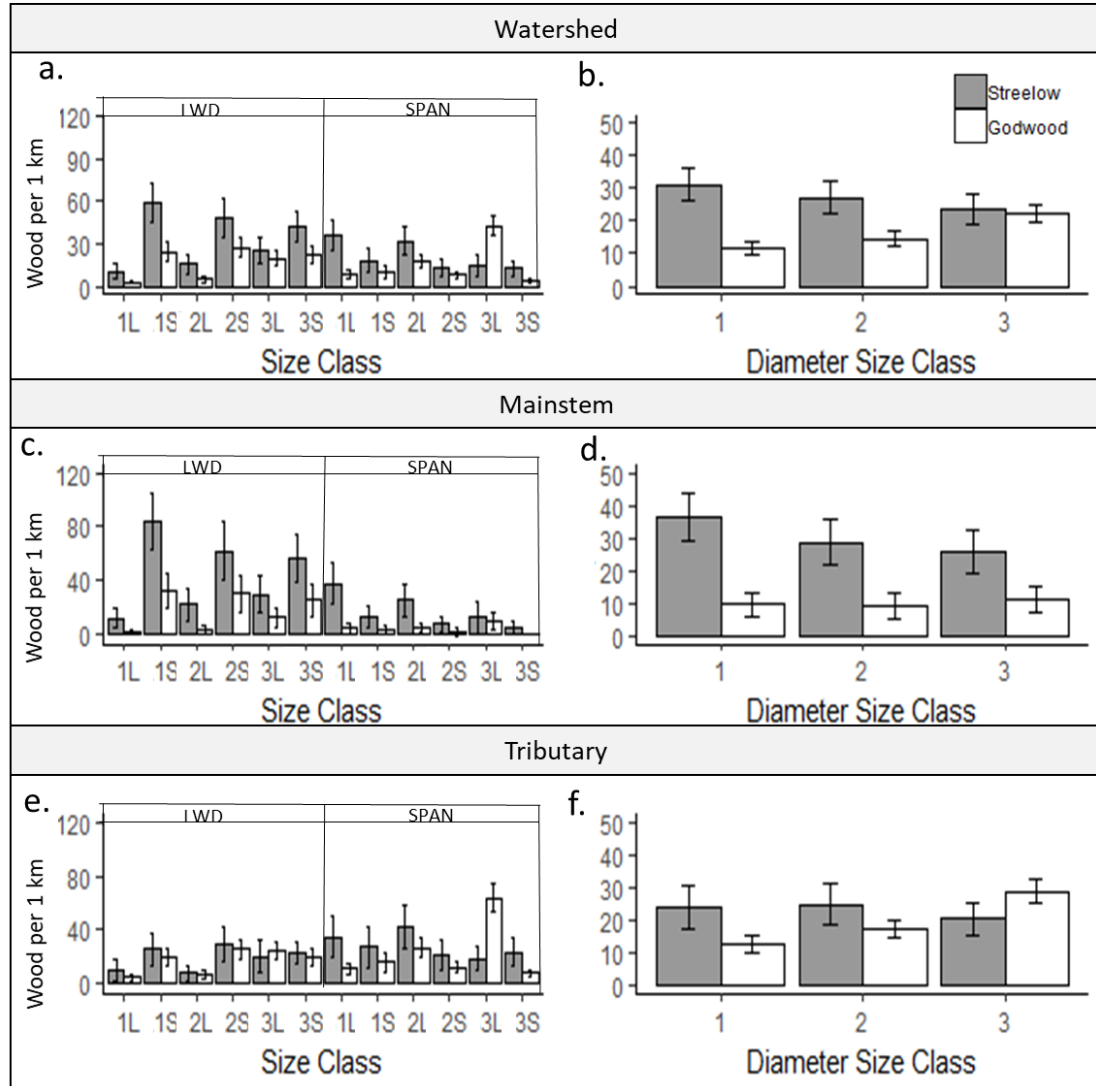


Figure 10. Comparison of the average number of woody debris pieces per km by size class between Streelow (logged) and Godwood Creek (unlogged) across the 2016 and 2017 field seasons. The wood in panels a, c, and e were categorized by wood type (1, 2 or 3 on x-axis), diameter size class (S or L on x-axis) and length size class (third letter). The wood type abbreviations are as follows: L = Large Woody Debris (LWD); S = Spanners (SPAN). Diameter size classes are: 1 = 15 – 30 cm; 2 = 30 – 50 cm; 3 = 50 cm+. Length size classes are: S = short (1 – 6 m); L = long (6 m+). The wood in panels b, d, and f are categorized by only diameter size class. Error bars = 95% CI.

Flow

The flow, or stream discharge (cfs), was low in both Streelow and Godwood. The flow was estimated as less than 1 cfs in all reaches except in the mainstem reaches of Godwood, where the flow was on average 2.82 cfs. The flow was 0.72 cfs in the mainstem reaches of Streelow. The flow was so low in paired reach 3 in Streelow that flow could not be measured, and therefore $Q \approx 0$.

Watershed temperature profiling

I calculated daily average temperatures and 7-day maximum and minimum temperatures at all scales over a 38-day period in the 2017 field season to determine differences between Streelow and Godwood. Daily average temperatures compared between mainstem and tributary reaches showed temperatures in Streelow averaging ~0.5 C° lower than Godwood (Figure 11). The fluctuations between maximum and minimum temperatures was small in both watersheds, between 11° and 14°C, with the temperatures in Streelow again ~ 0.5°C cooler than Godwood.

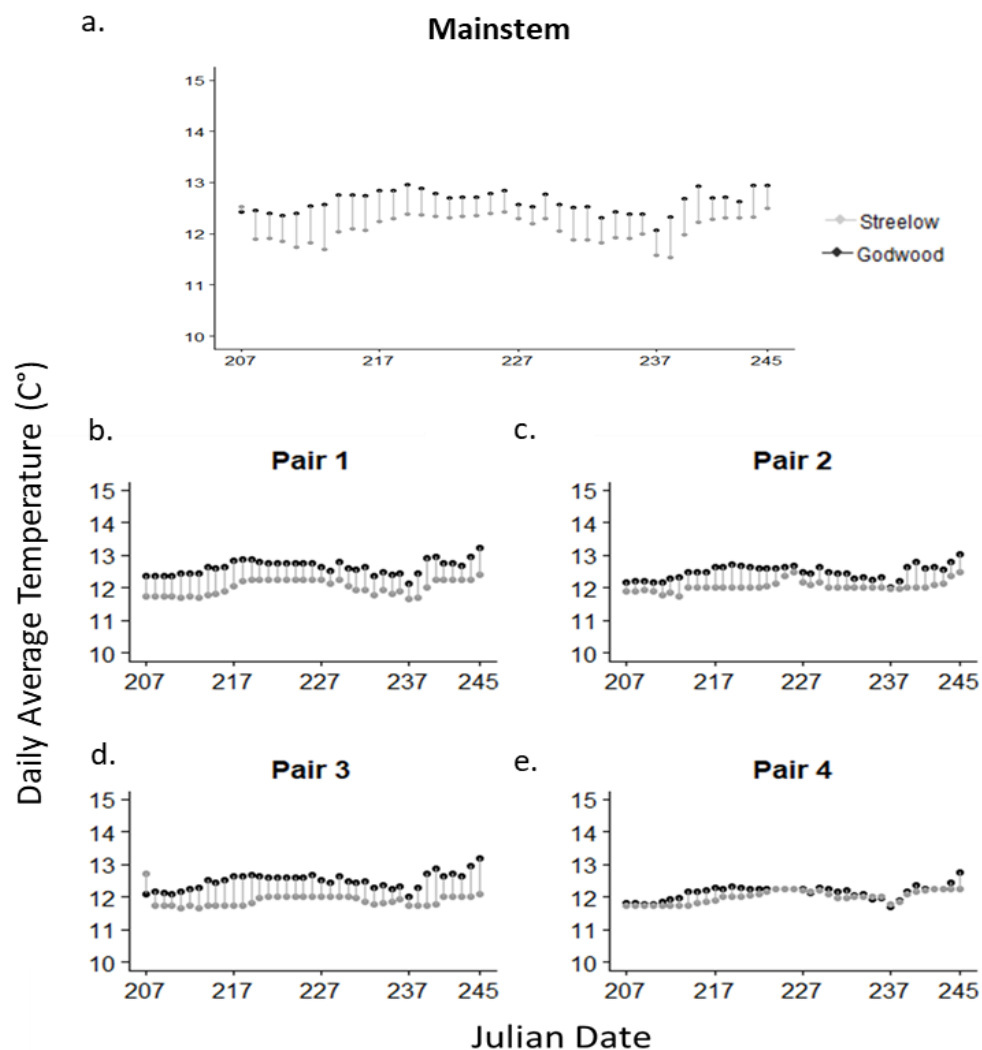


Figure 11. Daily average temperature profiles (C°) between mainstem (a) and paired tributary reaches (b-e) in Streelow (logged) and Godwood Creek (unlogged). Temperatures were recorded from July 26, 2017 (Julian date = 207) to Sept 2, 2017 (Julian date = 245), a total of 38 days.

Headwater Amphibian Results

Dicamptodon tenebrosus

D. tenebrosus were detected at 77% of sites in Streelow and 134 of 148 units in Godwood, with naïve occupancy estimates of 75% and 90.54%, respectively (Figure 12, Appendix D.1-D.2). Estimates of detection probability from the top models in the candidate model set were all high (≥ 0.90), with the top model estimating $p = 0.91$, meaning, if *D. tenebrosus* was present at a site, it would be detected on 91% of visits. In addition, estimates of occupancy from all top models in the candidate model set were high (≥ 0.99), suggesting that *D. tenebrosus* was present at essentially all surveyed sites. Though these are high occupancy estimates, naïve measures of occupancy agree with these high model-based estimates.

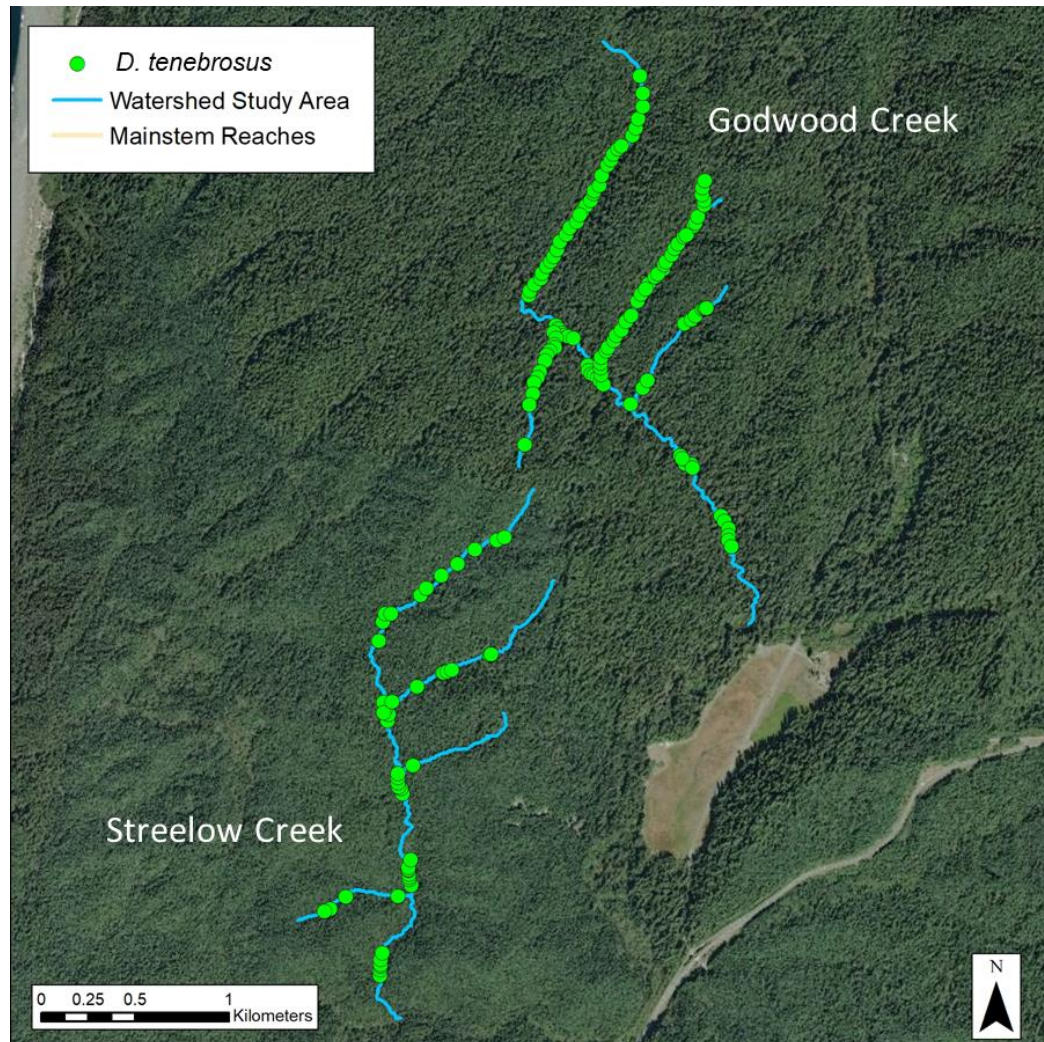


Figure 12. Distribution of *D. tenebrosus* detections at surveyed units in the Streelow (logged) and Godwood Creek (unlogged) watersheds during the 2016 and 2017 field season.

The top model from the candidate model set included 3 site-level covariates (Pair.ID, Coarse, and Wood) and one observation-level covariate (Tmax) (Table 2). Site-level covariate estimates from the top model showed large SE and large CI's that contained zero (Table 3). All top competing models (within 10 Δ AIC of top model) included the observation-level covariate Tmax (total survey time), but the estimates of

detection across the range of Tmax values were >0.95 . Similarly, across the range of all site-level covariates, the top models all predicted occupancy ≈ 1 . These model estimates were likely a product of the widespread distribution of *D. tenebrosus* throughout both watersheds resulting in a lack of association with any specific habitat type surveyed. In addition, the results of a parametric bootstrap test (X^2) used to check adequacy of the global model fit returned a significant p-value, suggesting a poor fit. I did not conduct further analysis or interpretation of the models because 1) the covariates were uninformative (likely because they were pretending variables), 2) the estimates of occupancy and detection probability were essentially 1, and 3) the model fit was poor. The high estimates of detection probability suggest that naïve estimates of *D. tenebrosus* occupancy reasonably represent the true occupancy at a site, and that conducting repeat surveys to estimate detection probability for this species may not be necessary.

Table 2. Single-species (*D. tenebrosus*), single-season occupancy model with pooled data from both years. Table displays k (number of parameters), AIC (Akaike Information Criterion), ΔAIC (relative difference in AIC), W_i (AIC model weights- relative likelihood of a model), and $accW_i$ (cumulative weight of models).

Model	K	AIC	ΔAIC	W_i	$accW_i$
p(Tmax)psi(Pair.ID+Coarse+Wood)	9	289.32	0.00	0.55	0.55
p(Tmax)psi(Pair.ID+Watershed+Wood+Grad)	10	290.15	0.83	0.37	0.92
p(Tmax)psi(Pair.ID+Watershed+Coarse)	9	294.21	4.90	0.05	0.97
p(obs+Tmax)psi(.)	9	295.56	6.24	0.02	0.99
p(.)psi(Pair.ID +Coarse+Wood)	8	300.38	11.06	0.00	1.00
p(.)psi(Pair.ID+Watershed+Wood)	8	300.89	11.58	0.00	1.00
p(.)psi(.)	2	323.53	34.21	0.00	1.00

Table 3. Parameter estimates (logit-scale) from the top model in the candidate model set of *D. tenebrosus* occupancy models.

Covariate	Beta	SE	CI
Pair.ID2	11.27	67.73	-121.47, 144.01
Pair.ID3	1.67	2.77	-3.76, 7.10
Pair.ID4	1.85	1.61	-1.31, 5.00
Pair.ID5	11.56	86.11	-157.21, 180.32
Coarse	4.14	1.78	0.64, 7.64
Wood	1.88	1.26	-0.60, 4.35
Tmax	0.86	0.27	0.33, 1.40

I calculated the relative index of abundance (maximum number of individuals detected at unit/unit area) of *D. tenebrosus* at all 236 units surveyed. The relative index of abundance of *D. tenebrosus* was higher in Godwood (median = 0.84, IQR = 0.94) than Streelaw (median = 0.73, IQR = 1.22) when compared at the tributary scale ($W = 1657.5$, $p = 0.048$), but the effect size was small (Cliff's delta = -0.21, 95% CI [-0.40, 0.00]). At the mainstem reach scale there was no difference (Streelaw median = 0.33; Godwood median = 0.32; $W = 1149.5$, $p = 0.816$; Cliff's Delta = -0.03, 95% CI [-0.25, 0.20]). Although there was not a large difference in the relative index of abundance between the watersheds, the number of units in Streelaw with a relative index of abundance of 0 (units where *D. tenebrosus* was not detected) was over twice the amount as in Godwood at both the mainstem and tributary reach scale (Figure 13).

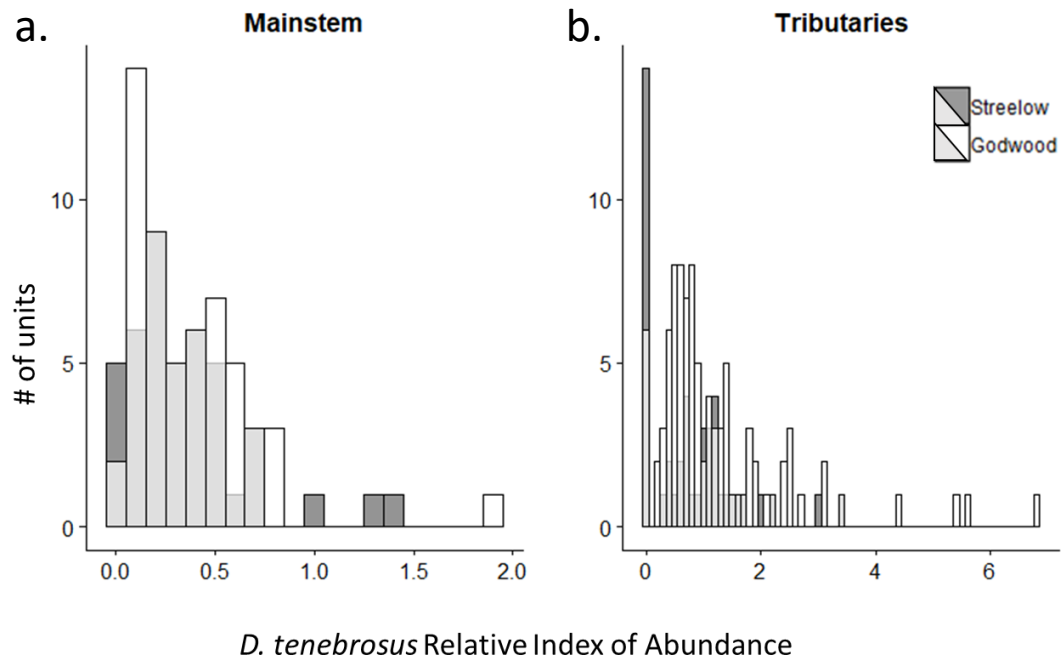


Figure 13. The distribution of *D. tenebrosus* relative index of abundance (number of individuals detected at unit/unit area) between the mainstem (a) and tributary reaches (b) of Streeflow (logged) and Godwood Creek (unlogged). The number of individuals was calculated as the maximum number of individuals detected at a unit (maximum during the initial and repeat surveys of both field seasons) and I calculated the area as the product of the unit length and the average unit width. The areas of overlap between Streeflow and Godwood Creek are represented in a light gray.

I graphically compared the distribution of *D. tenebrosus* Snout-Vent-Length (SVL) and the Body Condition Index (BOCI) between Streeflow and Godwood (Figure 14). The density distribution of SVL and BOCI were very similar in both watersheds, with most *D. tenebrosus* with an SVL around 25mm and BOCI around 0.04. Paedomorphic individuals found in Godwood represent the highest BOCI values (Figure 14-b).

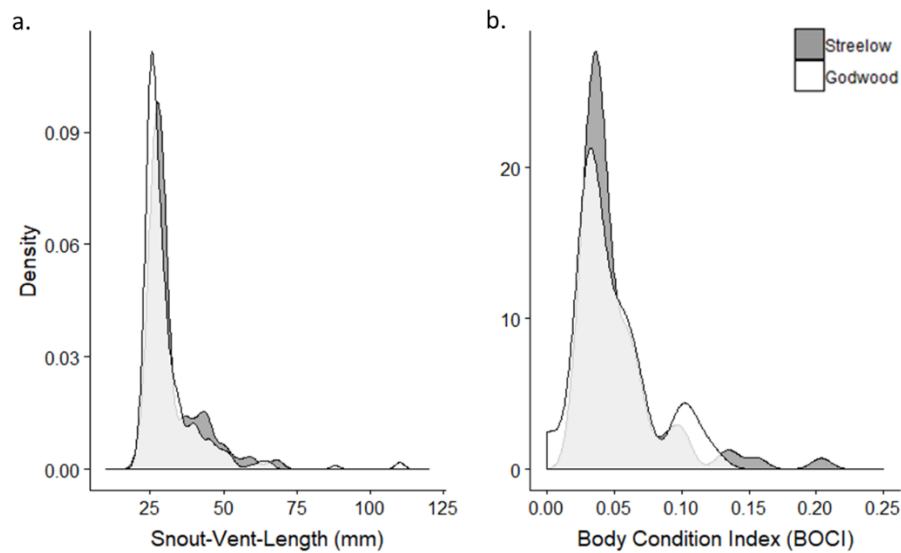


Figure 14. (a) Density distribution of *D. tenebrosus* Snout-Vent-Lengths (SVL) between Streelow (logged) and Godwood Creek (unlogged). (b) Distribution density of *D. tenebrosus* Body Condition Index (BOCI) between Godwood and Streelow Creek.

I compared the residuals from an ordinary least squares regression model of *D. tenebrosus* weight to Snout-Vent-Length (SVL). There was no difference in residuals at the watershed scale ($W = 2484.5$, $p = 0.135$; Cliff's delta = 0.152, 95% CI [-0.05, 0.34]), but the median residual in Godwood was less than 0 (median = -0.025) while in Streelow the median residual was above 1 (median = 0.03). Jakob et al. (1996) showed that positive residual values represent better body condition (higher than predicted) than a negative residual (lower than predicted).

Ascaphus truei

The estimate of detection probability (p) for *A. truei* from the top occupancy model (given that a site was occupied) was 0.369 when observation-level covariates were fixed at their mean value. With $p = 0.369$, I would expect that if an occupied site was surveyed

4 times (2 during 2016 and 2 during 2017), 15.8% of the time *A. truei* would not be detected. That probability drops dramatically if an occupied site were only surveyed once, with non-detection 63.1% of the time. MacKenzie et al. (2002) warns that detection probability estimates less than 0.5 tend to overestimate occupancy (Ψ) when the true value of $\Psi = 0.5$ or 0.7 but underestimate occupancy when $\Psi=0.9$. The top model estimated the probability that a site in Streelaw was occupied as 0.807 (95% CI [0.32, 0.97]) and as 0.993 (95% CI [0.63, 0.99]) in Godwood, when all other site-level covariates were fixed at their mean value across watersheds. When all covariates were fixed at their mean within watersheds, the top model estimated the probability that a site in Streelaw was occupied as 0.613 (95% CI [0.14, 0.94]) and as 0.996 (95% CI [0.43, 0.99]) in Godwood.

The top model from the candidate model set held a large portion of the weight ($W_i = 0.66$) and included four site-level covariates, Pair.ID, Watershed, Depth, and Coarse and one observation-level covariate, Tmax (Table 4). Estimates of occupancy were positively associated with Pair.ID5 (mainstem reaches), Godwood watershed, and coarse substrate, with the odds of occupancy 3.9 times greater in Pair.ID5, 34.4 times greater in Godwood and 2.4 times greater per 1 standard deviation increase in coarse substrate (Table 5). Occupancy was negatively associated with Pair.ID1-Pair.ID4 (tributary reaches), and depth. No tailed frogs were found in Pair.ID3 or 4 in either watershed (except 1 adult; Figure 15), and thus SE and CI estimates were large (Table 5). The parametric bootstrap test (X^2) used to check adequacy of the global model fit suggested a good fit ($p=0.485$).

Table 4. Top models of the *A. truei* single-species, single-season occupancy analysis. Table displays k (number of parameters), AIC (Akaike Information Criterion), Δ AIC (relative difference in AIC), W_i (AIC model weights- relative likelihood of a model), and $\text{acc}W_i$ (cumulative weight of models).

Model	k	AIC	Δ AIC	W_i	$\text{acc}W_i$
p(Tmax)psi(Pair.ID+Watershed+Depth+Coarse)	10	269.66	0.00	0.66	0.66
p(Tmax)psi(Pair.ID+Watershed+Depth)	9	271.58	1.92	0.25	0.92
p(Tmax)psi(Pair.ID+Watershed+Wood)	9	275.28	5.62	0.04	0.96
p(Tmax+Obs)psi(Pair.ID+Watershed+Coarse+Depth)	16	277.16	7.50	0.02	0.97
p(Tmax+Obs)psi(Pair.ID+Watershed+Coarse+Gravel)	16	277.39	7.74	0.01	0.99
p(Tmax)psi(Pair.ID+Watershed+Coarse)	9	280.47	10.81	0.00	0.99
p(.)psi(.)	2	356.67	87.01	0.00	1.00

Table 5. Parameter estimates (logit-scale) from the top model in the candidate model set of *A.truei* occupancy models.

Covariate	Beta	SE	CI
Pair.ID2	-3.12	1.47	-5.99, -0.22
Pair.ID3	-16.06	187.55	-383.64, 351.52
Pair.ID4	-14.41	116.59	-242.93, 214.12
Pair.ID5	1.36	1.31	-1.20, 3.91
Watershed2	3.54	1.48	0.64, 6.43
Depth	-1.79	0.69	-3.14, -0.44
Coarse	0.88	0.47	-0.04, 1.79
Tmax	0.83	0.23	0.37, 1.29

I created naïve occupancy maps in ArcGIS for a visual assessment of the distribution and occupancy of *A. truei* (Figure 15). In Streelaw, *A. truei* were only found at 6 survey units within mainstem reaches and were not found in any tributary reaches (Figure 15, Appendix D.3-D.4), and therefore I was not able to conduct a body condition index analysis or a relative index of abundance analysis between the watersheds. In Godwood, *A.truei* were found in all mainstem reaches and in 3 of the largest tributary reaches, although in one tributary reach only one adult tailed frog was found (Figure 15). Additionally, in Godwood, the highest occurrence of *A. truei* larva appear to be concentrated in the mainstem reaches and limited to the lower sections of the tributaries

(Figure 15). In only the largest and most northerly tributary of Godwood do *A. truei* larva detections continue to the uppermost headwater reaches (Figure 15). BOCI and total-length measurements pooled between watersheds and relative index of abundance estimates in Godwood are reported in Appendix A.

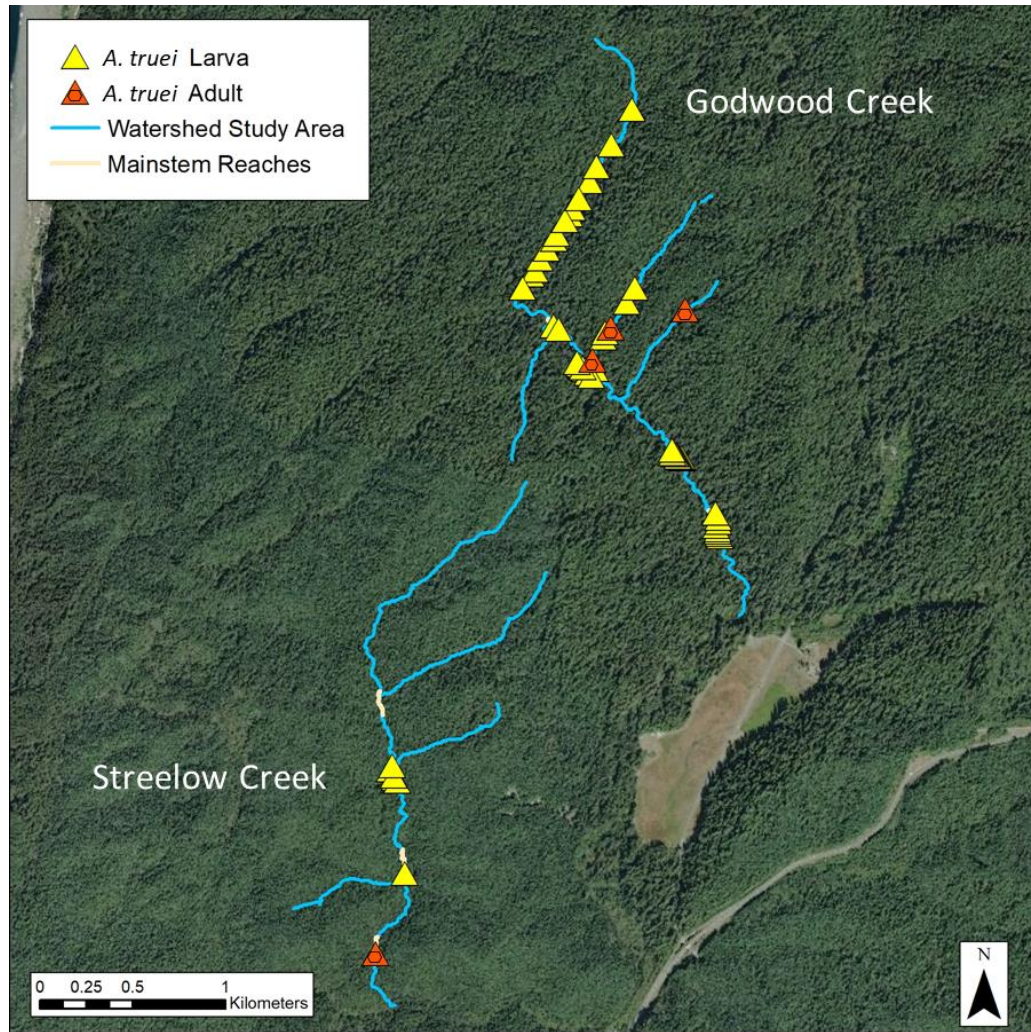


Figure 15. Distribution of *A. truei* detections at surveyed sites in Streelow (logged) and Godwood Creek (unlogged) during the 2016 and 2017 field season.

Rhyacotriton variegatus

I visited 22 seeps in Streelow and 35 seeps in Godwood, for a total of 57 seeps. Of the 22 seeps visited in Streelow, 3 were found in the mainstem reaches and 19 were found in the tributary reaches (Figure 16). Of the 35 seeps visited in Godwood, 6 of those seeps were in the mainstem reaches and 29 were in the tributary reaches (Figure 16). I detected *R. variegatus* in a total of 9 seeps in Streelow (naïve proportion occupied = 0.41) and 26 seeps in Godwood (naïve proportion occupied = 0.74) (Appendix D.5). Compared to *A. truei*, the distribution of *R. variegatus* was less concentrated in the mainstem reaches and extended into the uppermost headwater reaches of the tributaries (Figure 16). Each seep was surveyed once except for 4 seeps that I non-randomly surveyed twice. Surveys lasted from 1-50 min and time to first detection was 1-19 min (Appendix E). Initially, surveys were conducted so that all parts of detected seeps were thoroughly searched for *R. variegatus*, resulting in surveys lasting close to an hour. Later surveys ended after a *R. variegatus* was found or after 10 min of searching (Appendix E).

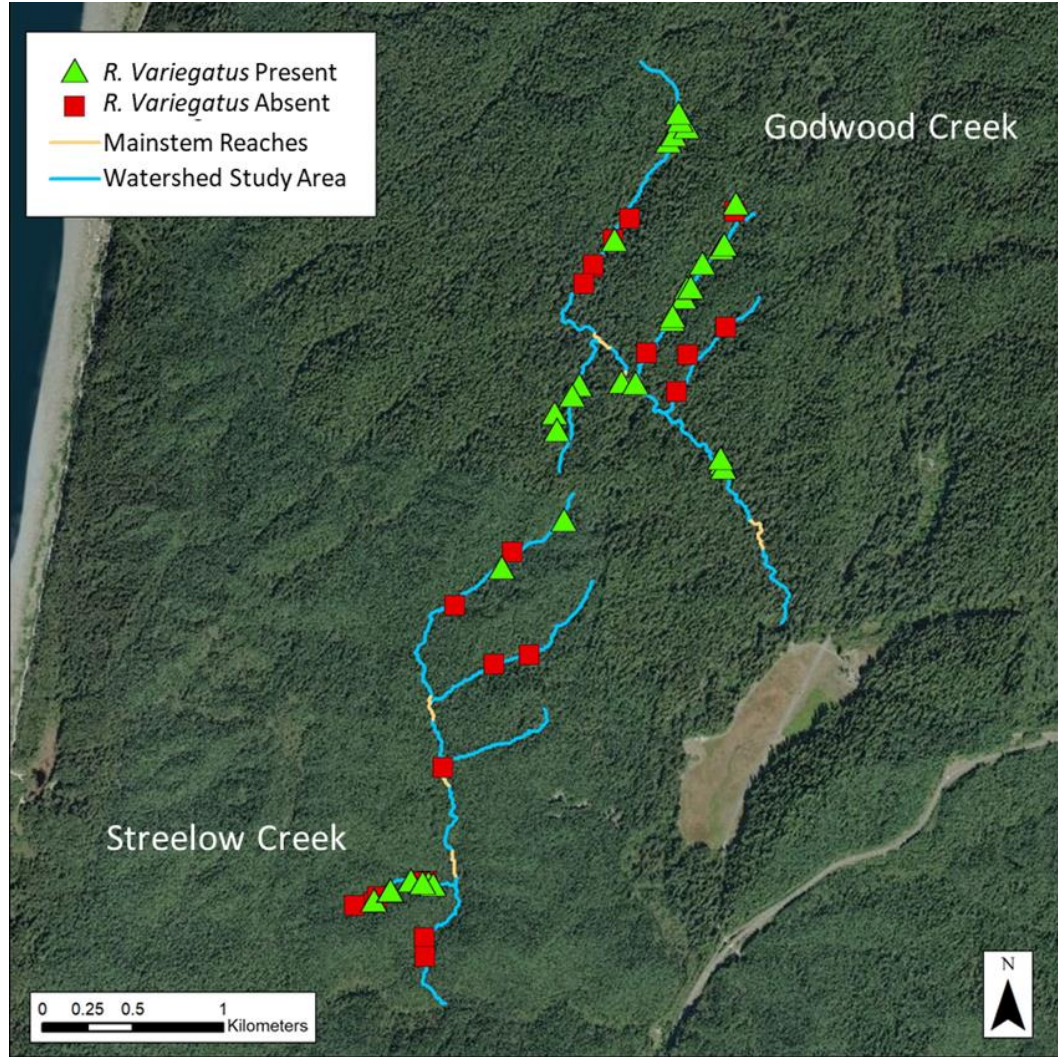


Figure 16. Distribution of *R. variegatus* detections at surveyed sites in Streelow (logged) and Godwood (unlogged) during the 2016 field season. The red squares represent a seep that was surveyed, but no *R. variegatus* were found. A green triangle represents a seep that was occupied by a least one *R. variegatus*. See Appendix F for locations of *R. variegatus* found within the channel.

I fit 18 models to the data including a global model with a total of 6 predictor variables (Watershed, Tier, Gravel, Coarse, Wood, and Grad; description of variables in Table 1). There were many top competing models (models within 2 Δ AICc from the top

model) and each model contained the variable Gravel (Table 6). I model-averaged the top 5 models which contained 70% of the model weight in the candidate model set and obtained estimates of each parameter from these models (Table 7). Results from the Hosmer-Lemeshow goodness of fit test for all top models were ≥ 0.05 . The 95% CI for all effects except for gravel contained zero and therefore there is little confidence that the effects of the variables Watershed, Tier, or Gradient were positive or negative. In addition, one of the models had an interaction effect between Watershed and Tier, but the SE and CI were very large (Table 7). Model averaged estimates predicted that for a 1% increase in Gravel cover, with all other covariates held at their mean value, the odds of seep occupancy increased by 1.03. Odds ratio = 1.03.

Table 6. Results of top logistic regression models from the candidate model sets.

Predictive habitat variables were fit to *R. variegatus* occupancy data. AICc values were used for model comparison and ranking. Additional values reported include k (number of fitted parameters), $\Delta AICc$, W_i (AICc weight), and $accW_i$ (cumulative AICc weight).

Model	k	AICc	$\Delta AICc$	W_i	$accW_i$
Occ ~ Watershed + Gravel	3	66.38	0.00	0.21	0.21
Occ ~ Watershed*Tier + Gravel + Grad	6	66.66	0.29	0.18	0.39
Occ ~ Gravel	2	67.37	1.00	0.13	0.52
Occ ~ Gravel + Grad	3	67.85	1.47	0.10	0.62
Occ ~ Gravel + Tier	3	68.06	1.68	0.09	0.71
Occ ~ Watershed + Gravel + Grad	4	68.40	2.02	0.08	0.78
Occ ~ Gravel + Course	3	68.80	2.42	0.06	0.85
Occ ~ 1	1	73.25	6.87	0.04	0.99

Table 7. Model averaging parameter estimates included in top candidate model set (all models within 2 $\Delta AICc$ of the top model).

Covariates	B	SE	CI
Gravel	0.03	0.01	0.01, 0.06
Gradient	-0.04	0.05	-0.13, 0.05
Tier2 (Mainstem reaches)	1.09	0.9	-0.68, 2.86
Watershed2 (Streelaw)	-1.12	0.63	-2.36, 0.12
Watershed2:Tier2	-35.52	448587	-8827.66, 8756.63

DISCUSSION

Impacts of past logging practices appeared to persist in Streelow, even 50 years after logging. These long-term impacts were evident in differences of headwater amphibian populations and the associated habitat characteristics between Streelow and the adjacent old-growth watershed, Godwood. Although no documentation of pre-harvest conditions exists for Streelow, I assumed that amphibian populations and stream characteristics were similar in the two watersheds before logging. However, inherent differences will exist because no two watersheds are exactly the same.

The watershed comparison of habitat characteristics showed that differences exist between Streelow and Godwood but because of their close spatial proximity there are also many similarities: orientation, drainage size, forest species composition and geology. This comparison revealed differences in valley-slope, valley-width, and wetted-width, with steeper valley-slopes, wider valley-widths and larger wetted-widths in Godwood, which could potentially affect sediment mobilization (i.e. slope stability and mass movement magnitude, frequency and type), flood hydrology, and the influence of debris flow from adjacent slopes (Hassan et. al. 2005a). However, a process-based classification system for headwater streams developed by Whiting and Bradley (1993) that utilizes variables including hillslope (valley-slope), channel gradient, valley-width, channel width (wetted-width), channel depth, and sediment size, suggests Streelow and Godwood have similar morphological types and therefore have similar dominant physical processes and rates of material movement into the stream channel and throughout the watershed

(Hassan et al. 2005a). There was no difference in stream gradient or unit gradient (streams were low gradient [$\sim 1^\circ$] in both watersheds), no difference in channel depth, and both watersheds had very low flows (<1 cfs). There were, however, differences in other habitat characteristics including substrate cover, woody debris, reach composition, canopy cover, overhang, and temperature, and these differences were likely a result of differences in logging history. Despite differences in logging history, Streelaw and Godwood are physically and functionally (i.e. movement of sediment) very similar and provide a reliable design for quantifying the long-term impacts of past logging practices on headwater amphibians and their associated habitat characteristics.

The most evident impacts of past logging were seen in the difference of substrate cover, woody debris, and reach composition between the watersheds. There were higher amounts of sediment cover in Streelaw at all scales, and the median sediment cover was 22% lower in Godwood. Additionally, coarse substrate cover was much lower in Streelaw at all scales, with the median cover of coarse material 38% higher in Godwood. Assuming substrate cover in Streelaw was similar to present conditions in Godwood, it is likely that high sediment inputs into the channel from past logging practices have covered the original coarse stream bed cover, eliminating critical habitat for many aquatic biota including amphibians, invertebrates and fish (Beschta 1978, Hicks et al. 1991, Welsh and Hodgson 2008). The movement and storage of sediment inputs is largely impacted by the associated woody debris in and around the stream channel (Keller et al. 1985)

There were greater amounts of woody debris in all size classes in the mainstem of Streelaw. This result is inconsistent with findings from Sedell et al. (1988), where

streams flowing through young-growth and recently-harvested areas contained fewer woody debris pieces than streams running through mature old-growth stands. In the tributary reaches, there were more small-diameter woody debris (size class 1) in Streelow, but more large-diameter woody debris (size class 3) in Godwood. Surprisingly, there was no difference in the amount of large-diameter woody debris at the watershed scale, but this result may be due to the largest diameter size class (50 cm +) including both extremely large old growth trees that were 200 cm in diameter and younger trees that were 50 cm in diameter. Had I classified the extremely large old-growth trees in a new size class, differences may have been evident at the watershed scale. In small headwater streams, relatively small woody debris can form log jams and relatively large woody debris can create an accumulation of sediment causing the stream flows to run subsurface (Jackson and Sturm 2002).

High proportions of tributary reaches in Streelow were subsurface, buried or pocket channel, which essentially eliminated the potential for headwater amphibian habitat. Tributary reach composition of subsurface, pocket or buried was twice the amount in Streelow (66%) as compared to Godwood (34%). A stream running subsurface, or becoming buried, was observed in tributary reaches in Godwood, mainly in the uppermost headwater reaches, but the amount of subsurface and buried sections in Streelow was much larger. Furthermore, long 'sediment plugs' (likely caused by the excess wood) existed in the tributary reaches, where the channel would not reappear for over 100 m, and when the channel did appear again it would show high levels of fine sediment cover. Long subsurface sections existed in Godwood, but the main difference

was when the channel resurfaced again, it was not choked with sediments, and coarse substrate was present.

Canopy cover was high in both watersheds but was greater in Streelow, with over half of the samples at >91% canopy cover. In addition, % overhang was lower in Streelow at all scales. The Streelow watershed's forest regenerated without any management such as thinning, and it appears that as a result, a dense forest regrew that lacked the complexity of old-growth stands, including gaps in the canopy caused by large fallen trees. The lack of open canopy reduced the amount of light that reached the understory, likely reducing understory growth (i.e., % overhang).

The relationship between the inherent characteristics of Streelow (low stream gradient, steep valley-slopes, weakly consolidated geology, high precipitation, tectonic activity) and the logging-impacted habitat characteristics (high sediments loads, high amounts of woody debris, and high amounts of subsurface, buried and pockets sections) is complex, with all variables connected and potentially compounding the effects of the others, specifically the balance between production and transportation of sediment. For example, all flow regimes have a maximum amount of sediment, or maximum capacity, that can be transported, and the ability to transport sediment is dependent on stream power (potential and kinetic energy). Stream power is reduced in low-gradient headwater streams, and therefore stream capacity, because these streams have decreased potential and kinetic energy (Mount 1995) and low flow accumulation even in heavy rain events (Jackson and Sturm 2002). Reduced stream capacity in these low gradient headwater streams can result in amplification of impacts from logging practices such as

sedimentation (i.e. retention of fine sediments) (Murphy and Hall 1981, Corn and Bury 1989). Additionally, in headwater streams, the retention of sediment is largely associated with the amount and size of woody debris that can store large amounts of sediment and delay its transport for extended periods (Bisson et al. 1987). Rivers usually transport less than their capacity because the sediment input from the watershed is less (Mount 1995), but in streams like Streelaw where variables affecting sediment are compounded and interacting, the capacity of the stream has likely been surpassed.

Lastly, stream temperature was consistently around 0.5°C lower in Streelaw, the logged watershed. This result is contrary to most findings, where water temperature increases after logging has occurred (Bury and Corn 1988). However, because the watershed has experienced 50 years of natural recovery, including natural regeneration of the forest, the dense second-growth forest canopy has likely reduced the stream temperature because of reduced light penetration. Welsh and Hodgson's (2008) findings indicate that for streams to support viable populations of headwater amphibians, stream temperatures should not exceed 15 °C for *R. variegatus*, 15.8 °C for *A. truei*, and 20.9 °C for *D. tenebrosus*. The 7-day mean maximum and minimum temperatures in Godwood and Streelaw both are within the threshold to support viable populations of all three headwater amphibian populations studied here.

Of the three headwater amphibians, *A. truei* appeared to be the most sensitive to long-term impacts of logging, such as increased sediment, and were patchily distributed throughout the watersheds. The variable 'Coarse' was included in the top *A. truei* occupancy model and was highly negatively correlated with the variable 'Sediment': the

more coarse substrate present, the less sediment there was, and vice-versa. The model showed coarse substrate had a positive effect on *A. truei* occupancy, and therefore a negative effect of sediment on occupancy. These associations of coarse and sediment on *A. truei* occupancy are consistent with the literature (Diller and Wallace 1999, Ashton et al. 2006); however, gradient was not included in the top models, but is often predictive of *A. truei* occurrence (Diller and Wallace 1999, Welsh and Hodgson 2008, Wahbe and Bunnell 2003). In this study, the absence of this effect is likely a result of the extremely low gradient of the watersheds even in sections of fast-water, where *A. truei* was usually found.

The high amounts of sediment in Streelaw appear to greatly limit the distribution and occupancy of *A. truei* larva, such that they were only detected in 6 units in the mainstem reaches (Appendix D.3-D.4). In addition, the low amount of available habitat and open channel, also appears to greatly reduce the distribution, occupancy and relative abundance of *A. truei* throughout Streelaw (Appendix C). Though the distribution, occupancy, and relative abundance of *A. truei* was drastically less in Streelaw than in Godwood, these data support a hypothesis suggested by Diller and Wallace (1999) in which *A. truei* do not appear to be constrained to old-growth habitats *per se*; instead, there are specific habitat requirements (i.e. unembedded coarse substrate) that are more likely to exist in undisturbed watersheds.

D. tenebrosus were much more widely distributed than *A. truei*, and naïve occupancy and occupancy model estimates suggest that *D. tenebrosus* occupied areas with higher sediment loads. Because of their wide-spread distribution throughout both

watersheds and their high occupancy rates, no measured habitat variables predicted *D. tenebrosus* occupancy well, concurrent with the findings by Welsh and Hodgson (2008). This suggests that although *D. tenebrosus* are ecologically very important and can be good indicators of disturbances such as logging, using measurements of occupancy alone may not be sufficient to indicate long-term effects of logging. Additionally, *D. tenebrosus* may also recover more rapidly from logging disturbance due to their ability to disperse from neighboring source populations. It is possible that *D. tenebrosus* habitat quality was lower in Streelaw than Godwood but that the populations in Streelaw are maintained by immigration from surrounding high-quality habitat, a hypothesis I could not test directly with this study design.

The relationship between *R. variegatus* occupancy and sediment was less obvious; however, occupancy of *R. variegatus* was lower in Streelaw than Godwood, with no occupied seeps found along the mainstem. Gravel was the only variable found to influence the presence of *R. variegatus* in seeps, and this likely due to gravel being a core component of the formation of seeps. Unfortunately, resurveys were not conducted at seeps due to their sensitive nature, but there is potential to use time-to-detection survey designs to provide a solution that does not require repeat surveys (Bornand et al 2014). Time-to-detection models can estimate detectability and occupancy, have been used throughout various ecology disciplines and warrant further investigation into the usefulness for estimating detectability and occupancy for sensitive amphibian species.

Although the negative effect of sediment on headwater amphibian occupancy is not a novel result, a key finding of this study is that the high amounts of sediment in

Streelow have persisted in the watershed 50 years after logging, and these effects appear to continue to influence occupancy of at least two amphibian species. The sediment accumulation in Streelow has likely covered much coarse substrate, essentially eliminating critical habitat for headwater amphibians, especially *A. truei* larvae. Fine sediment is a common substrate in streams of all types of management histories, especially in low gradient streams, but the current sediment load of Streelow is likely much higher than its pre-harvest state and appears to have surpassed the capacity of the stream to move sediment out of the system.

Restoration Recommendations

Despite the apparent persistent degraded state of Streelow habitat conditions, successful restoration of Streelow (determined through further amphibian population and habitat characteristic surveys post restoration) seems attainable. Although there is low occupancy and distribution of *A. truei*, it is encouraging to see that all three headwater amphibian species that were present in Godwood also persisted in Streelow. Therefore, source populations exist and are available locally to respond to restoration and may be used to guide restoration.

More specifically, GPS locations of seeps occupied by *R. variegatus* should be utilized (and have been provided to RNSP) during restoration efforts of Streelow such that large equipment is excluded from those areas. These exclusion zones should allow for the persistence of important source populations of *R. variegatus* during restoration efforts through the reduction of direct harm and preservation of suitable habitat. In

addition, because *R. variegatus* are a species of special concern, surveys should be conducted for *R. variegatus* in the immediate vicinity or adjacent areas that could be affected by restoration actions despite whether I had previously found *R. variegatus* in those areas. To further ensure the preservation of and reduce accidental take of *R. variegatus*, I suggest if any suitable habitat (seep with gravel or coarse substrate) is detected, efforts should be made not to disturb that habitat. In addition to using source population locations to decide on equipment exclusion zones, they can also be used to prioritize areas that could be restored and are close to source populations, making recolonization more likely.

I found that the most important key structural habitat quality associated with headwater amphibians was unembedded coarse substrate. Unembedded coarse substrate is very important to amphibians (Welsh and Hodgson 2008), fish (Cederholm et al. 1981) and aquatic invertebrates (Wood and Armitage 1997). Therefore, if restoration efforts of Streelaw are based on the habitat needs or preferences of headwater amphibians (and therefore many other biota), restoration efforts should reduce the input of sediments into the stream channel and increase the presence of coarse substrate. Since coarse substrate in Streelaw likely still exists underneath the accumulated sediment, the removal and reduction of sediment input should be a focus of restoration efforts.

The dominant natural source of sediment input in small forested streams, such as Streelaw and Godwood, are rapid mass wasting and bank erosion, with little contribution from common processes such as surface erosion and soil creep (Hassan et al. 2005a). In harvested basins, ditches, roads, and skid tracks surfaces are the main source of fine

sediment into stream channels (Hassan et al. 2005a). Although access to Streelow via existing roads will be extremely useful during restoration efforts, actions to restore or decommission roads that could increase the input of sediment into channels would likely benefit headwater amphibians. Additionally, the removal of the large sediment plugs in the tributary reaches of Streelow that appear to be preventing the natural transport of sediment down through the watershed could potentially help the movement and subsequent removal of sediment.

Although *A. truei* have not been found in the tributary reaches and would therefore not be directly impacted by restoration in the tributaries (i.e., operation of large equipment), the potential for increased sediment inputs from restorations efforts could affect *A. truei* in the mainstem reaches. With the evidence of the sensitivity of *A. truei* to high sediment loads, caution should be taken during restoration and efforts should be made to reduce the amount of sediment that is released into the watershed at any one time. If key sediment plugs can be identified in the upper headwater reaches and are slowly removed prior to large rain events, Streelow could potentially resume natural recovery. In addition, consideration of removing excess wood in Streelow while still retaining complexity should be considered. Attitudes towards removing, keeping or adding wood to stream networks have changed over the last 100 years, including the currently-used management technique of adding woody debris to stream channels (Sedell and Luchessa 1982). However, for a low gradient headwater stream like Streelow, where woody debris greatly affected the transport and storage of sediment (Hassan et al. 2005b),

there is potential that too much woody debris in the stream channel could further impede recovery.

Focusing on the most sensitive species, *A. truei* and *R. variegatus*, will provide more insight into the effects of logging on watersheds. *D. tenebrosus* should continue to be included in studies such as this one because differences in relative abundance may indicate watershed health, but areas such as pools, slack water, or any area without coarse substrate likely do not warrant repeat surveys, depending on monitoring program goals. The assumption that $p = 1$ for *D. tenebrosus* in these watersheds appeared reasonable given my results. Continued monitoring of headwater amphibian populations should be a priority of this restoration project after efforts are completed, with a focus on fast-water sections with coarse substrate that could support *A. truei*. An increase in distribution and occupancy of sensitive species such as *A. truei* after restoration actions are completed could suggest restoration actions are working. Continued monitoring of any other species (i.e. salmonids, steelhead, or aquatic insects) for which baseline population data exist should also continue after restoration actions are completed. The importance of an ecosystem-wide approach for successful restoration projects must be emphasized.

Through comparison of headwater amphibian populations and the associated habitat characteristics between the Streelaw and Godwood watersheds, I found evidence of persistent long-term impacts from historical logging practices in Streelaw. Similar to the results of Ashton et al. (2006), my research suggests that the recovery of some headwater amphibian populations in northwestern California may take decades after disturbance from historical logging practices, while others (such as *D. tenebrosus*) may

recover more quickly. Because of unique characteristics in Streelow, including low gradient channels, increased in-channel LWD and slash and highly erodible geology, the impacts from logging will likely persist indefinitely without active restoration efforts.

Headwater streams, much like headwater amphibians, are important to the entire stream network and are sensitive to disturbance and warrant attention during restoration projects.

Headwater amphibians can provide indications of immediate (Bury 1983) and long-term (Ashton et al. 2006, Corn and Bury 1989, this study) disturbances in small headwater streams, areas where fish cannot reach.

MANAGEMENT IMPLICATIONS

This study contributes data and analysis valuable to the understanding of the long-term effects of logging in a forested watershed ecosystem, and provides managers with a study design that can accurately measure the magnitude of logging impacts in forested watershed systems. Although this study is limited to one watershed that has been impacted by logging, the results from this study can have broad implications for other watersheds with similar characteristics such as low gradient, first- or second-order headwater streams, steep valley-slopes, and naturally erodible geology. Natural recovery after logging can be impeded in streams with similar characteristics due to excessive sediment inputs, and therefore may require active restoration actions, such as removal of sediment. Additionally, headwater streams in particular are extremely important to the health of the stream network as a whole including the survival of fish and other biota downstream (Meyer et al. 2007, Moore and Richardson 2003, Wipfli et al. 2007, Welsh 2011), and therefore should be a focus of watershed managers.

This study also provides valuable baseline data for restoration efforts in Streelaw and allows for assessment of restoration efforts success through continued monitoring of amphibian populations. *A. truei* and *R. variegatus* should be the focus of future monitoring in Streelaw because they appear to be the most sensitive to long-term impacts from logging. Although these amphibians are sensitive to changes in their environment, they also appear resilient and able to persist or recolonize areas after massive disturbances such as historical logging.

REFERENCES

- Adams, M. J., and R. B. Bury. 2002. The endemic headwater stream amphibians of the American northwest: associations with environmental gradients in a large forested preserve. *Global Ecology and Biogeography* 11: 169-178.
- Ashton, D. T., S. B. Marks, and H. H. Welsh. 2006. Evidence of continued effects from timber harvesting on lotic amphibians in redwood forests of northwestern California. *Forest Ecology and Management* 221 (183-193).
- Beschta, R. L. 1978. Long-term patterns of sediment production following road construction and logging the Oregon Coast Range. *Water Resource Research* 14(6):1011-1016.
- Best, D. W. 1995. History of timber harvest in the Redwood Creek basin, northwestern California. U.S. Geological Survey Professional Paper 1454, pp. C1-C7.
- Bisson, P. A., R. E. Bilby, M. D. Bryant, C. A. Dolloff, G. B. Grette, R. A. House, M. L. Murphy, K. V. Koski, and J. R. Sedell. 1987. Large woody debris in forested streams in the Pacific Northwest: past, present, and future. In *Streamside management, forestry and fishery interactions*. Institute of Forest Research, University of Washington Seattle.
- Bornand, C. N., M. Kery, L. Bueche, and M. Fischer. 2014. Hide-and-seek in vegetation: time-to-detection is an efficient design for estimating detectability and occurrence. *Methods in Ecology and Evolution*.

- Burkholder, L. L. and L. V. Diller. 2007. Life History of Postmetamorphic Coastal Tailed Frogs (*Ascaphus truei*) in Northwestern California. *Journal of Herpetology* 44(2):251-262.
- Burnham, K.P. and D. R. Anderson. 2002. Model selection and Multimodel Inference. Springer-Verlag, New York.
- Bury, R. B. 1983. Differences in amphibian populations in logged and old growth redwood forest. *Northwest Science* 57(3):167-178.
- Bury, R. B. and M. J. Adams. 1999. Variation in Age at Metamorphosis across a Latitudinal Gradient for the Tailed Frog, *Ascaphus truei*. *Herpetologica* 55:2(283-291).
- Bury, R. B. and P. S. Corn. 1988. Response of aquatic and streamside amphibians to timber harvest: a review. In K. J Raedeke (ed.). *Streamside Management: Riparian Wildlife and Forestry Interactions*, pp. 165-180. University of Washington, Institute of Forest Resources, Contribution 59, Seattle.
- Bury, R. B. and P. S. Corn. 1991. Sampling methods for amphibians in stream in the Pacific Northwest. USDA Forest Service, General Technical Report PNW-GTR-275. Pacific Northwest Research Station. Portland, Oregon.
- Cannata, S., R. Henly, J. Erler, J. Falls, D. McGuire and J. Sunahara. 2006. Redwood Creek Watershed Assessment Report: Section IV Prairie Creek Subbasin. North Coast Watershed Assessment Program.
- Cashman, S. M., M. Kelsey, and D. R. Harden. 1995. Geology of the Redwood Creek Basin, Humboldt County, CA. *Geomorphic Processes and Aquatic Habitat in the*

Redwood Creek Basin, Northwestern CA. U.S. Geological Survey Professional Paper 1454-B.

Cederholm, C. J., L. M. Reid, and E. O. Salio. 1981. Cumulative effects of logging road sediment on salmonid populations in the Clearwater River, Jefferson County, Washington. In Presented to the conference salmonid spawning gravel: a renewable resource in the Pacific Northwest? State of Washington Water Resources Center. Washington State University.

Chamberlin, T.W., R. D. Harr and F. H. Everest. 1991. Timber harvesting, silviculture, and watershed processes. Pages 181-205 in Influences of forest and rangeland management on salmonid fishes and their habitats.

Corn, P. S., and R. B. Bury. 1989. Logging in western Oregon: Response of headwater habitats and stream amphibians. *Forest Ecology and Management* 29:39-57.

Cummins, K. W. 1962. An evaluation of some techniques for the collection and analysis of benthic samples with special emphasis on lotic waters. *The American Midland Naturalist* 67:2 (477-504).

Davic, R. D., and H. H. Welsh, Jr. 2004. On the Ecological Roles of salamanders. *Annual Review of Ecology, Evolution, and Systematics* 35:405-34.

Diller, L. V. and R. L. Wallace. 1996. Distribution and habitat of *Rhyacotriton variegatus* in managed, young growth forests in north coastal California. *Journal of Herpetology* 30:184-191.

- Diller, L. V. and R. L. Wallace. 1999. Distribution and Habitat of *Ascaphus truei* in Streams on Managed, Young Growth Forests in North Coastal California. *Journal of Herpetology* 33(1):71-79.
- Dobriyal, P., R. Badola, C. Tuboi, and S. A. Hussain. 2017. A review of methods for monitoring streamflow for sustainable water resource management. *Applied Water Science* 7: 2617-2628.
- Fiske, I. J. and R. B. Chandler. 2011. Unmarked: An R Package for Fitting Hierarchical Models of Wildlife Occurrence and Abundance. *Journal of Statistical Software*. 43:10.
- Fiske, I. J. and R. B. Chandler. 2017. Overview of Unmarked: An R Package for the Analysis of Data from Unmarked Animals. <https://cran.r-project.org/web/packages/unmarked/index.html>. Viewed 8 Nov 2017.
- Ford, L. S. and D. C. Cannatella. 1993. The major clades of frogs. *Herpetological Monographs* 7:94-107.
- Freeman, M. C., C. M. Pringle, and C. R. Jackson. 2007. Hydrologic connectivity and the contribution of stream headwaters to ecological integrity at regional scales. *Journal of the American Water Resources Association* 43(1): 5-14.
- Frost, T. M., S. R. Carpenter, and T. K. Kratz. 1992. Choosing Ecological Indicators: Effects of Taxonomic Aggregation on Sensitivity to Stress and Natural Variability. In: McKenzie D.H., Hyatt D.E., McDonald V.J. (eds) *Ecological Indicators*. Springer, Boston, MA.

- Garrard, G. E., S. A. Bekessy, M. S. McCarthy and B. A. Wintle. 2008. When have we looked hard enough? A novel method for setting minimum survey effort protocols for flora surveys. *Austral Ecology* 33: 986-998.
- Good, D. A. and D. B. Wake. 1992. Geographic variation and speciation in the torrent salamanders of the genus *Rhyacotriton* (Caudata: Rhyacotritonidae). University of California Publications in Zoology 126:1-91.
- Hassan, M. A, M. Church, T. E. Lisle, F. Brardinoni, L. Benda, and G. E. Grant. 2005*a*. Sediment transport and channel morphology of small, forested streams. *Journal of the American Water Resource Association* 41:853-876.
- Hassan, M. A, D. L. Hogan, S. A. Bird, C. L. May. T. Gomi, and D, Campbell. 2005*b*. Spatial and temporal dynamics of wood in headwater streams of the Pacific Northwest. *Journal of the American Water Resources Association* 41:899-919.
- Hayes, M. P, T. Quinn, D. J. Dugger, T. L. Hicks, M. A. Melchiors, and D. E. Runde. 2006. Dispersion of Coastal Tailed Frog (*Ascaphus truei*): An Hypothesis relation occurrence of frogs in non—fish-bearing headwater basins to their seasonal movement. *Journal of Herpetology* 40(4): 531-543.
- Hicks, B. J., J. D. Hall, P. A. Bisson, and J. R. Sedell. 1991. Responses of Salmonids to Habitat Changes. *American Fisheries Society Special Publication* 19:486-518.
- Intermountain Environmental Inc. (IEI). 2016. Flow Discharge using the Float Method.
- Jackson, S. D. 2003. Ecological Considerations in the Design of River and Stream Crossings. In *Proceedings of the International Conference on Ecology and Transportation*, edited by C. Leroy Irwin, Paul Garrett, and K.P. McDermott.

- Raleigh, NC: Center for Transportation and the Environment, North Carolina State University, 2003. 10 pp.
- Jackson, C. R., and C. A. Sturm. 2002. Woody debris and channel morphology in first- and second-order forested channels in Washington's coast ranges. *Water Resources Research* 38(9):1177.
- Jakob, E. M., S. D. Marshall, and G. W. Uetz. 1996. Estimating fitness: a comparison of body condition indices. *Oikos* 77(1):61-67.
- Johnston, B., and L. Frid. 2002. Clearcut logging restricts the movements of terrestrial Pacific giant salamanders (*Dicamptodon tenebrosus* Good). *Canadian Journal of Zoology* 80:2170-2177.
- Keller, E. A., A. MacDonald, T. Tally, and N. J. Merritt. 1985. Effects of large organic debris on channel morphology and sediment storage in selected tributaries of Redwood Creek. In "Geomorphic Processes and Aquatic Habitat in the Redwood Creek Drainage Basin." USGS Prof. Pap. Washington Off., Washington, D.C. In press.
- Kondolf, G. M, S. Anderson, R. Lave, L. Pagano, A. Merenlender, and E. S. Bernhardt. 2007. Two Decades of River Restoration in California: What can we learn? *Restoration Ecology* 15(3):516-523.
- Lele, S. R, Keim J. L., and P. Solymos. 2019. ResourceSelection: Resource Selection (Probability) Functions for Use-Availability Data. R package version 0.3-4. <https://CRAN.R-project.org/package=ResourceSelection>.

- Leonard, W., H. A. Brown, L. L. C. Jones, K. R. McAllister and R. M. Storm. 1993. Amphibians of Washington and Oregon. Seattle Audubon Society, Seattle, Washington.
- Lufkin, A. 1996. California's salmon and steelhead. Berkeley: University of California Press.
- MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83(8):2248-2255.
- Madej, M. A. 1995. Changes in channel-stored sediment, Redwood Creek, Northwestern California, in: Nolan, K. M., H. M. Kelsey, and D. C. Marron (eds.), *Geomorphic processes and aquatic habitat in the Redwood Creek basin, Northwestern California*, U.S. Geological Survey Professional Paper 1454, p. O1-027.
- Madej, M. A., H. Ambrose, D. Currens, and S. Hadden. 2006. Assessing changes in stream health following watershed restoration: A 30-year perspective, Redwood Creek Basin, Humboldt County, California. Arcata, CA.
- May, C. W., R. R. Horner, J. R. Karr, B. W. Mar, and E. B. Welch. 1999. Effects of Urbanization on small streams in the Puget Sound ecoregion. *Watershed Protection Techniques* 2(4):483-494.
- Matsuda, B. M., and J. S. Richardson. 2005. Movement patterns and relative abundance of coastal tailed frogs in clearcuts and mature forest stands. *Canadian Journal of Forestry* 35: 1131-1138.

- Mazerolle, M. J. 2017. AICcmodavg: model selection and multimodel inference based on (Q) AIC (c). R package version 2.1-1. <https://cran.r-project.org/package=AICcmodavg>.
- Metter, D. E. 1964. A morphological and ecological comparison of two populations of the tailed frog *Ascaphus truei*. *Copeia* 1964:181-195.
- Meyer, J. L., D. L. Strayer, J. B. Wallace, S. L. Eggert, G. S. Helfman, and N. E. Leonard. 2007. The contribution of headwater streams to biodiversity in river networks. *Journal of the American Water Resources Association* 43(1):86-103.
- Moore, R. D., and J. S. Richardson. 2003. Progress towards understanding the structure, function and ecological significance of small stream channels and their riparian zones. *Canadian Journal of Forest Research* 33:1349-1351.
- Mouillot, D., N. A. J. Graham, S. Villéger, N. W. H. Mason, and D. R. Bellwood. 2013. A functional approach reveals community responses to disturbances. *Trends in Ecology and Evolution* 28(3):167-177.
- Mount, J. F. 1995. California rivers and streams: the conflict between fluvial process and land use. University of California Press, Berkeley.
- Moyle, P., R. Lusardi, P. Samuel, and J. Katz. 2017. State of the Salmonids: Status of California's Emblematic Fishes 2017. Center for Watershed Sciences, University of California, Davis and California Trout, San Francisco, CA. 579 pp.
- Murphy, M. L., and J. D. Hall. 1981. Varied effects of clear-cut logging on predators and their habitat in small streams of the Cascade Mountains, Oregon. *Canadian Journal of Fisheries and Aquatic Sciences* 38:137-145.

- National Research Council. 1992. Restoration of Aquatic Ecosystems: Science, Technology and Public Policy. National Academy Press, Washington, D.C.
- Niemi, G. J., and M. E. McDonald. 2004. Ecological indicators. Annual Review of Ecology, Evolution, and Systematics 35:89–111.
- Nussbaum, R. A., E. D. Brodie, Jr., and R. M. Storm. 1983. Amphibians and reptiles of the Pacific Northwest. University of Idaho Press, Moscow, Idaho.
- Parker, M. S. 1994. Feeding Ecology of stream-dwelling Pacific giant salamander larvae (*Dicamptodon tenebrosus*). Copeia 1994:705-718.
- Quinn, T., M. P. Hayes, D. J. Dugger, T. L. Hicks, and A. Hoffman. 2007. Comparison of two techniques for surveying headwater stream amphibians. The Journal of Wildlife Management 71(1):282-288.
- Redwood National and State Parks (RNSP). 1999. General Management Plan: Humboldt and Del Norte Counties California.
- Redwood National and State Parks (RNSP). 2007. Environmental Assessment: Streelow Creek Fish Passage.
- Resetarits, W. J. Jr., and J. Bernardo. 1998. Experimental ecology: issues and perspectives. Oxford University Press, New York. pp. 113-132.
- Resh, V. H., A. V. Brown, A. P. Covich, M. E. Gurtz, H. W. Li, G. W. Marshall, S. R. Reice, A. L. Sheldon, J. B. Wallace, R. C. Wissmar. 1988. The role of disturbance in stream ecology. Journal of the North American Benthological Society 7(4):433-455.

- Richardson, J. S. and R. J. Danehy. 2006. A synthesis of the ecology of headwater streams and their riparian zones in temperate forests. *Forest Science* 53(2):131-147.
- Russell, K. R., T. J. Mabee, M. B. Cole, and M. J. Rochelle. 2005. Biotic and abiotic influences on salamanders: evaluating biotic and abiotic influences on torrent salamanders in managed forests of western Oregon. *Nongame Research and Management* 33(4):1413-1424.
- Russell, W., J. Sinclair, and K. H. Michels. 2014. Restoration of Coast Redwood (*Sequoia sempervirens*) Forest through Natural Recovery. *Open Journal of Forestry* 4(2):16-111.
- Sedell, J. R., and K. J. Luchessa. 1982. Using the historical record as an aid to salmonid habitat enhancement. In *Acquisition and utilization of aquatic habitat inventory information*: 210-223. Armantrout, N. A. (Ed.). Bethesda, MD: American Fisheries Society, Western Division.
- Sedell, R. J., P. A. Bisson, F. J. Swanson, and S. V. Gregory. 1988. What we know about large trees that fall into streams and rivers, in C. Maser, R. F. Tarrant, J. M. Trappe, and J. F. Franklin (Eds), *From the Forest to the Sea: A Story of Fallen Trees*, USDA Forest Service General Technical Report, PNW-GTR-229, 47-81.
- Seney, J and M. A. Madej. 2015. Soil Carbon Storage Following Road Removal and Timber Harvesting in Redwood Forests. *Earth Surface Processes and Landforms* 40(15):2084-2092.

- Sparkman, M. D., W. G. Duffy, and T. R. Moore. 2014. FRGP Report: Prairie Creek Monitoring Project. Fisheries Restoration Grants Program. (Project Number: P1010302).
- Stebbins, R. C. 2003. A Field Guide to Western Reptiles and Amphibians. 3rd ed. Houghton Mifflin Co., Boston.
- Strahler, A. N. 1957. Quantitative analysis of watershed geomorphology. Geological Society of America Bulletin 63(6):977-981.
- Strickler, G. S. 1959. Use of the densiometer to estimate density of forest canopy on permanent sample plots. PNW Old Series Research Notes No. 180, p. 1-5.
- Symonds, M. R. E., and A. Moussalli. 2011. A brief guide to model selection, multimodel inference and model averaging in behavioral ecology using Akaike's information criterion. Behavioral Ecology and Sociobiology 65:13-21.
- Tait, C. K. and L. V. Diller. 2006. Life History of the Southern Torrent Salamander (*Rhyacotriton variegatus*) in Coastal Northern California. Journal of Herpetology 40(1):43-54.
- Torchiano, M. 2017. effsize: Efficient Effect Size Computation. R package version 0.7.1. <https://CRAN.R-project.org/package=effsize>.
- United States Geological Survey [USGS]. 2017. National Water Information System: Web Interface. <https://waterdata.usgs.gov/nwis>. Accessed July 5, 2017.
- Vlaming, V. L. de, and R. B. Bury. 1970. Thermal selection in tadpoles of the tailed frog *Ascaphus truei*. Journal of Herpetology 4:179-189.

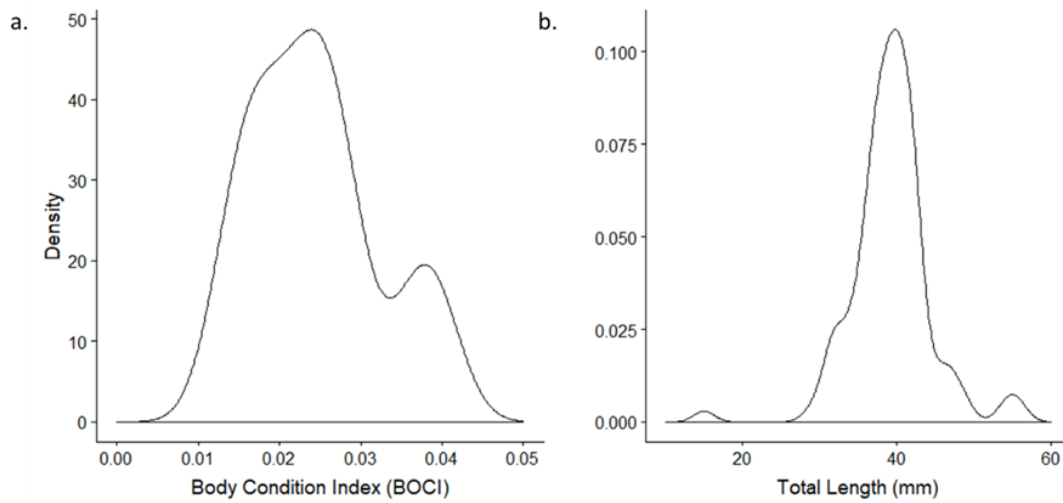
- Wahbe, T. R., and F. L. Bunnell. 2003. Relations among larval tailed frogs, forest harvesting, stream microhabitat, and site parameters in southwestern British Columbia. *Canadian Journal of Forestry Restoration* 33:1256-1266.
- Wahbe, T. R., F. L. Bunnell, and R. B. Bury. 2004. Terrestrial movements of juvenile and adult tailed frogs in relation to timber harvest in coastal British Columbia. *Canadian Journal of forest Research* 34(12):2455-2466.
- Welsh, H. H. 2011. Frogs, fish, and forestry: An integrated watershed network Paradigm conserves biodiversity and ecological services.
- Welsh, H. H. and A. J. Lind. 1996. Habitat Correlates of the Southern Torrent Salamander, *Rhyacotriton variegatus* (Caudata: Rhyacotritonidae), in Northwestern California. *Journal of Herpetology* 30(3):385-398.
- Welsh, H. H. and G. R. Hodgson. 2008. Amphibians as metrics of critical biological thresholds in forested headwater streams of the Pacific Northwest, U.S.A. *Freshwater Biology* 53:1470-1488.
- Welsh, H. H. and L. M. Ollivier. 1998. Stream amphibians as indicators of ecosystem stress: a case study from California's redwoods. *Ecological Applications* 8:1118-1132.
- Welsh, H. H., K. L. Pope, and C. A. Wheeler. 2008. Using multiple metrics to assess the effects of forest succession on population status: A comparative study of two terrestrial salamanders in the US Pacific Northwest. *Biological Conservation* 141: 1149-1160.

- Whiting, P. J., and J. B. Bradley. 1993. A process-based classification system for headwater streams. *Earth Surface Processes and Landforms* 18: 603-6012.
- Wilzbach, M. A. 2016. State of the Fisheries and Aquatic Resource of Prairie Creek: Final Report to Redwood National and State Parks (Cooperative Agreement Number: P14AC01284).
- Wipfli, M. S., J. S. Richardson, and R. J. Naiman. 2007. Ecological Linkages Between Headwaters and Downstream Ecosystems: Transport of Organic Matter, Invertebrates, and Wood Down Headwater Channels. *Journal of the American Water Resources Association* 43(1):72-85.
- Wood, P. J., and P. D. Armitage. 1997. Biological effects of fine sediment in the lotic environment. *Environmental Management* 21(2):203-217.

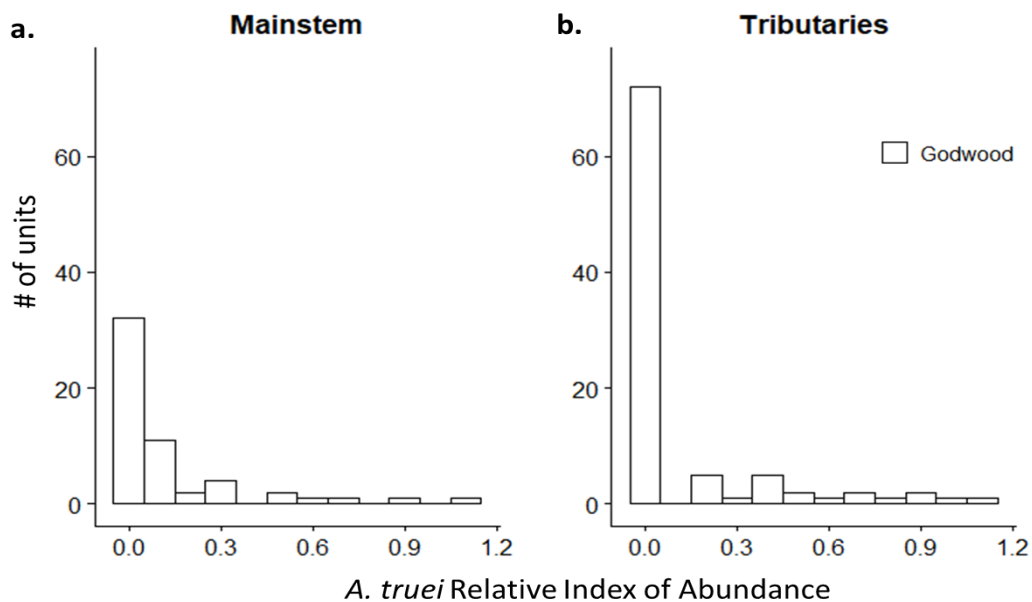
APPENDICES

Appendix A: *A. truei* Body Condition Index (BOCI), total-length and Relative Index of Abundance graphs.

Appendix A.1: Density distribution of a) Body Condition Index (BOCI) and b) total-length (mm) of *A. truei*. Both plots show data pooled from Streeflow (logged) and Godwood Creek (unlogged) watersheds.



Appendix A.2: Distribution of *A. truei* relative index of abundance (number of individuals detected at unit/unit area) between mainstem and tributary reaches in Godwood Creek (unlogged). The number of individuals was calculated as the maximum number of individuals detected at a unit (maximum during the initial and repeat surveys of both field seasons) and I calculated the area as the product of the unit length and the average unit width.



Appendix B: Tables with survey dates and number of surveys at each reach.

Appendix B.1: Summary of the survey dates (A = amphibian surveys, H = habitat surveys), number of units surveyed, and number of repeat surveys conducted each paired mainstem reach in the 2016 field season. Repeat surveys were conducted in approximately 40% of mainstem units in both watersheds.

2016 MAINSTEM								
Pair ID	Streelow (logged)				Reach	Godwood (unlogged)		
	Reach	Dates	#units	# repeat surveys		Dates	#units	# repeat surveys
5	1	6/6-8 (A) 6/6 (H)	12	5	1	5/22-31 (A) 5/19 (H)	14	5
5	2	6/8-9 (A&H)	11	3	2	5/24-6/1 (A) 5/19 (H)	13	7
5	3	6/9-10 (A&H)	11	3	3	5/31-6/1 (A) 5/20 (H)	14	5
5	4	6/10-14 (A) 6/8 (H)	9	5	4	5/31-6/3 (A) 5/20 (H)	14	5
Total			43	16	Total			55 22

Appendix B.2: Summary of the survey dates (A = amphibian surveys, H = habitat surveys), number of units surveyed, and number of repeat surveys conducted each paired tributary reach in the 2016 field season. Although repeat surveys were not officially conducted in tributary reaches, a few were conducted near the confluence.

2016 TRIBUTARIES								
Pair ID	Streelow (logged)				Reach	Godwood (unlogged)		
	Reach	Dates	#units	# repeat surveys		Dates	#units	# repeat surveys
1	TE6	6/26-28 (A)	22	1	TE4	6/13-26 (A&H)	36	3
2	TE5	6/29-30 (A&H)	11	0	TE3	6/13-7/6 (A) 6/13&7/2 (H)	29	3
3	TE4	7/1 (A&H)	2	0	TE2	7/7-12 (A&H)	17	0
4	TNW 1	7/13 (A&H)	10	0	TSW 2	7/15 (A&H)	11	0
Total			45	1	Total			93 6
Σ			88	17	Σ			148 28

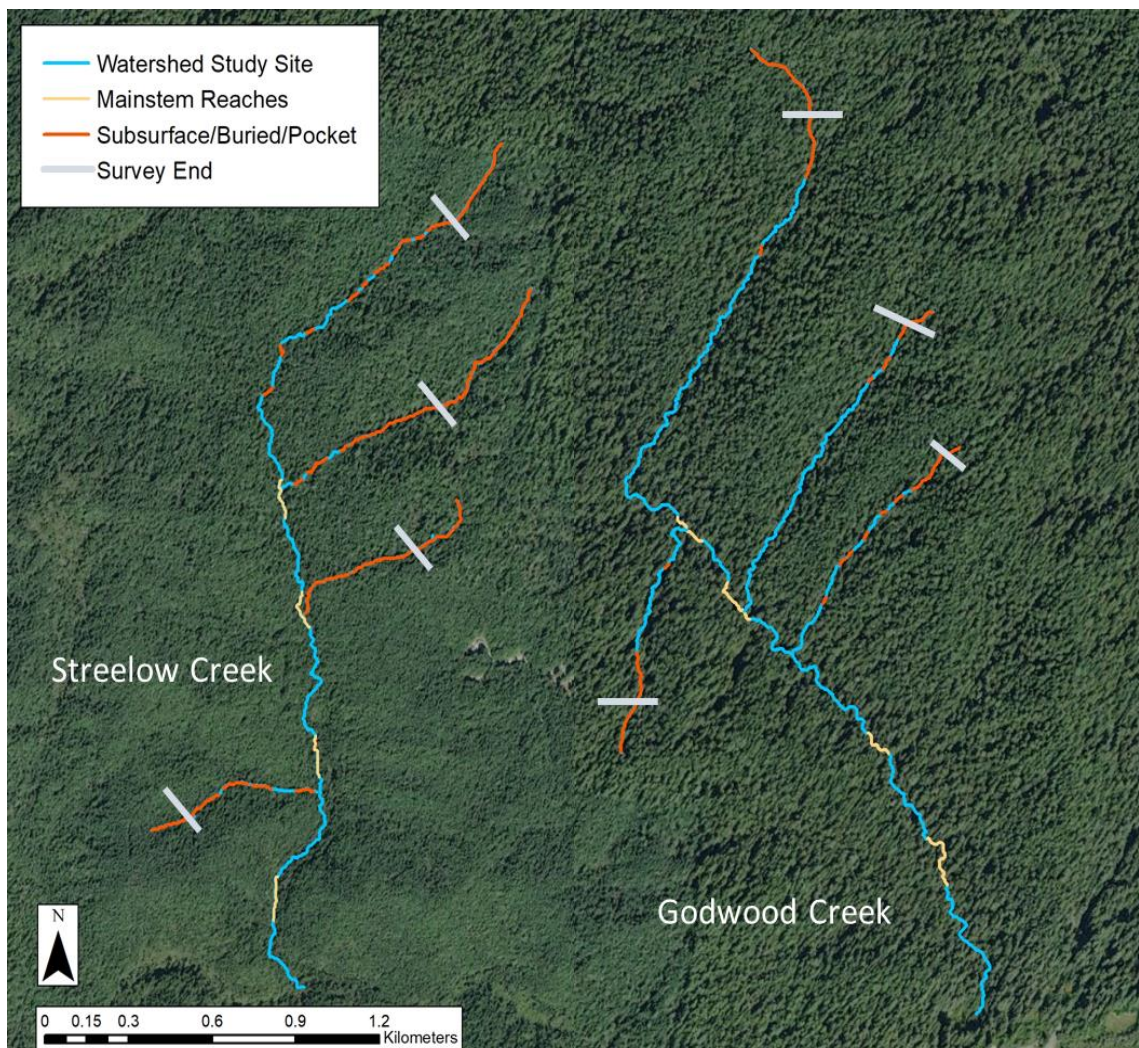
Appendix B.3: Summarization of the survey dates (only amphibian surveys were conducted in 2017), number of units surveyed, and number of resurveys conducted the paired mainstem reaches in the 2017 field season. I conducted a 100% resurvey of mainstem units.

2017 MAINSTEM									
Streelow (logged)					Godwood (unlogged)				
Pair ID	Reach	Dates	#units	#resurvey	Reach	Dates	#units	#resurvey	
5	1	7/6-7	4	4	1	7/8-10	4	4	
5	2	7/11-13	4	4	2	7/10-12	4	4	
5	3	7/11-13	4	4	3	7/12	4	4	
5	4	7/18	4	4	4	7/17-19	4	4	
Total			16	16	Total			16	16

Appendix B.4 Summarization of the survey dates (only amphibian surveys were conducted in 2017), number of units surveyed, and number of resurveys conducted each paired tributary reach in the 2017 field season. I did not conduct resurveys in tributaries reaches.

2017 TRIBUTARIES									
Streelow (logged)					Godwood (unlogged)				
1	TE6	7/25	7	0	TE4	8/9	11	0	
2	TE5	8/3-8/8	7	1	TE3	8/7	8	0	
3	TE4	7/18-8/3	2	1	TE2	7/17-19	6	1	
4	TNW1	7/20	4	0	TSW2	7/24	4	0	
Total			20	2	Total			29	1
Σ			36	18	Σ			45	17

Appendix C: Map of Streeflow (logged) and Godwood (unlogged) study area with areas that were subsurface, buried or pocket denoted with red. Grey bars denote where I stopped surveying. Compared to the mainstem reaches, the tributary reaches in both watersheds had higher proportions of subsurface, buried and pocket channel types. In Streeflow, about a third of the tributary channels were open and two-thirds were subsurface, buried or pocket. In Godwood, two-thirds of tributary channels were open, and a third were subsurface, buried, or pocket. Most of the open sections in the tributary reaches of Streeflow were concentrated near the confluence with the mainstem. Most of the subsurface, buried and pocket sections in Godwood were only evident in the uppermost headwater reaches of the watershed and were interspersed with open channel.



Appendix D: Indices tables of amphibian naïve occupancy and abundance.

Appendix D.1: The number of sites where a *D. tenebrosus* was detected versus the number of units surveyed, and the total number of *D. tenebrosus* found within paired reaches during the 2016 field season and compared between Streelow (logged) and Godwood Creek (unlogged). Paired reaches 1-4 are tributary reaches and paired reach 5 is mainstem reaches.

2016 Field Season: <i>D. tenebrosus</i>				
	# of Occupied Units		# of <i>D. tenebrosus</i>	
	Streelow	Godwood	Streelow	Godwood
Pair 1	11/22	35/36	27	111
Pair 2	11/11	25/29	27	73
Pair 3	2/2	11/17	2	22
Pair 4	5/10	11/11	8	30
Pair 5	39/43	52/55	167	292
<i>Total</i>	68/88	134/148	231	428

Appendix D.2: The number of sites where a *D. tenebrosus* was detected versus the number of units surveyed, and the total number of *D. tenebrosus* found within paired reaches during the 2017 field season and compared between Streelow (logged) and Godwood Creek (unlogged). Paired reaches 1-4 are tributary reaches and paired reach 5 is mainstem reaches.

2017 Field Season: <i>D. tenebrosus</i>				
	# of 'Occupied' Units		# of <i>D. tenebrosus</i>	
	Streelow	Godwood	Streelow	Godwood
Pair 1	4/7	10/11	15	32
Pair 2	4/4	8/8	23	24
Pair 3	2/2	6/6	7	18
Pair 4	4/4	4/4	12	14
Pair 5	14/18	16/16	73	97
<i>Total</i>	28/35	44/45	130	185

Appendix D.3: The number of sites where an *A. truei* was detected versus the number of units surveyed, and the total number of *A. truei* found within paired reaches during the 2016 field season and compared between Streelow (logged) and Godwood Creek (unlogged). Paired reaches 1-4 are tributary reaches and paired reach 5 is mainstem reaches. * indicates animals that were not found during an official survey.

2016 Field Season: <i>A. truei</i>				
	# of 'Occupied' Units		# of <i>A. truei</i>	
	Streelow	Godwood	Streelow	Godwood
Pair 1	0/22	13/36	0	21
Pair 2	0/11	4/29	0	7
Pair 3	0/2	0/17	0	1*
Pair 4	0/10	0/11	0	0
Pair 5	2/43	23/55	2	86
Total	2/88	40/148	2	115

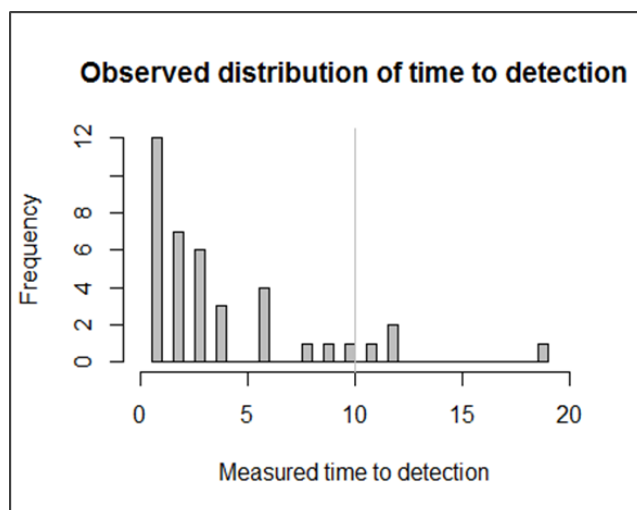
Appendix D.4: The number of sites where an *A. truei* was detected versus the number of units surveyed and the total number of *A. truei* found within paired reaches during the 2017 field season and compared between Streelow (logged) and Godwood Creek (unlogged). Paired reaches 1-4 are tributary reaches and paired reach 5 is mainstem reaches.

2017 Field Season: <i>A. truei</i>				
	# of 'Occupied' Units		# of <i>A. truei</i>	
	Streelow	Godwood	Streelow	Godwood
Pair 1	0/7	3/11	0	7
Pair 2	0/4	2/8	0	7
Pair 3	0/2	0/6	0	0
Pair 4	0/4	0/4	0	0
Pair 5	4/16	8/16	4	25
Total	4/33	13/45	4	39

Appendix D.5: The number of seeps where *R. variegatus* (RHVA) was detected or not and the total numbers of *R. variegatus* found during in-channel surveys (i.e. *D. tenebrosus* and *A. truei* surveys). Compared at the paired reach scale between Streelow (logged) and Godwood Creek (unlogged) during the 2016 field Season. Paired reaches 1-4 are tributary reaches and paired reach 5 is mainstem reaches.

2016 <i>R. variegatus</i> detections						
	# 'Occupied' Seeps		# 'Unoccupied' Seeps		# In Channel RHVA	
	Streelow	Godwood	Streelow	Godwood	Streelow	Godwood
Pair 1	2	7	2	4	0	1
Pair 2	0	9	2	2	0	6
Pair 3	0	0	1	3	0	8
Pair 4	7	4	5	0	0	5
Pair 5	0	6	3	0	0	4
Total	9	26	13	9	0	24

Appendix E: Time to first detection of *R. variegatus* in all surveyed seeps. The vertical line depicts the decision to start constraining surveys to 10 minutes due to excessive time spent searching seeps.



Appendix F: Distribution of *R. variegatus* detections at surveyed sites in Streelow (logged) and Godwood Creeks (unlogged) during the 2016 Field season. The red squares represent a seep that was surveyed but no *R. variegatus* was found. A light-green triangle represents a seep that was occupied by at least one *R. variegatus*. A dark-green triangle represents *R. variegatus* that were found in the stream channel during a *D. tenebrosus* and *A. truei* survey.

